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BRITISH MUSEUM (NATURAL HISTORY)

HANDBOOK OF
R. H. BURNE'S
CETACEAN DISSECTIONS

LONDON
1952





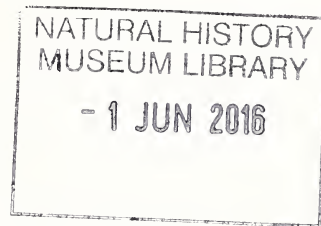
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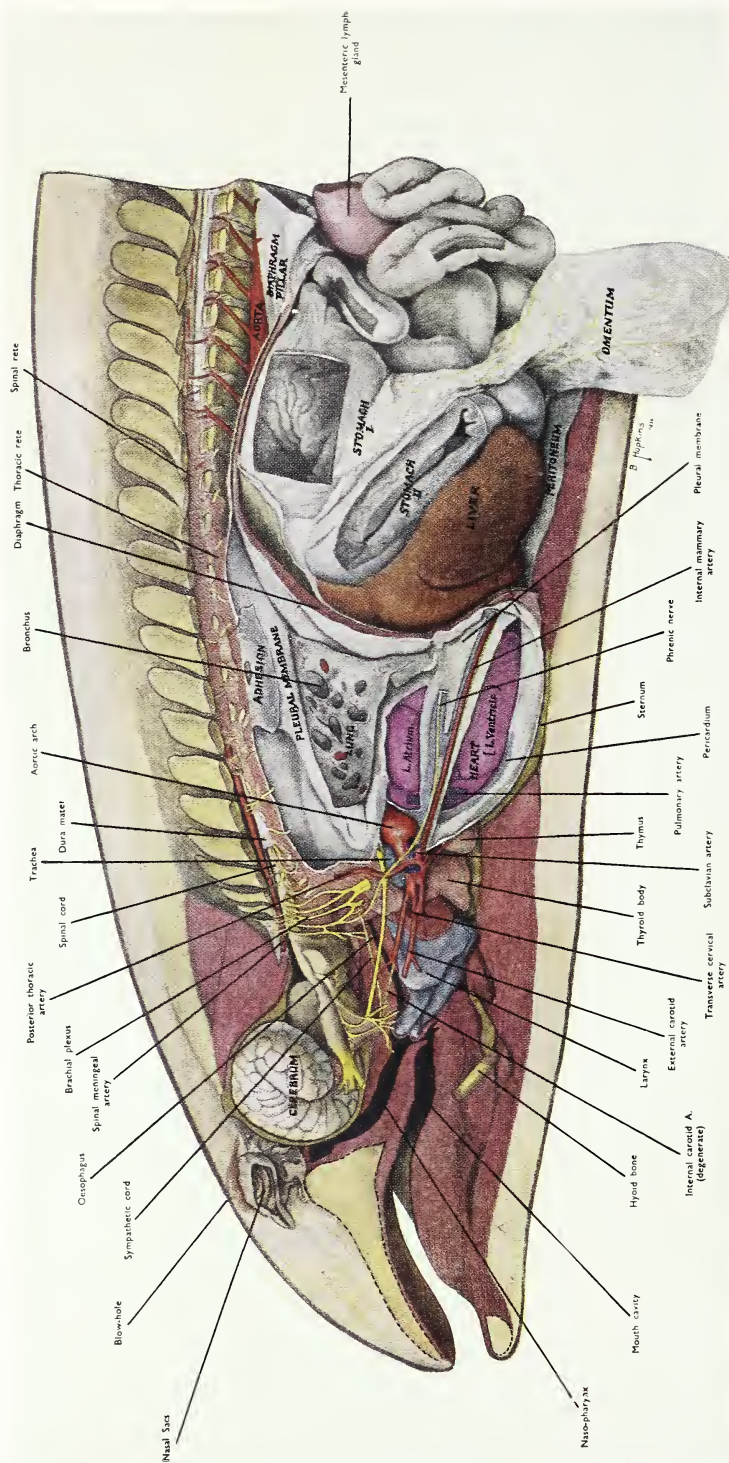


FIG. 1. Dissection of the front half of the body of a porpoise, *Phocaena phocaena*; with the skeleton and soft tissues removed to the middle plane and the greater part of the left lung cut away.

PREFACE

IN 1935 Mr. R. H. Burne, M.A., F.R.S., joined the British Museum (Natural History) as a voluntary scientific worker and generously undertook to prepare dissections illustrating cetacean anatomy for exhibition in the Whale Hall. He not only applied the experience of forty years' comparative anatomical work at the Royal College of Surgeons to the Museum's great benefit by producing a noteworthy series of preparations, but also made coloured explanatory diagrams, arranged the lay-out of the exhibits and wrote most of the descriptive labels.

The outbreak of war in 1939 interrupted the task which Mr. Burne had set himself and, later, impairment of his sight made it impossible for him to add to what he had already done. For the valuable preparations now on exhibition the Museum owes a great debt of gratitude to Mr. Burne, and the present handbook is published not only as an acknowledgment but to ensure that his work may be available to a wider public than can visit the Museum.

The figures illustrating the handbook are, with few exceptions, either reproductions of the coloured diagrams or photographs of the actual dissections. Of the exceptions figure 1 is from a diagram executed in colour by Miss B. Hopkins under Mr. Burne's supervision. Figure 2 and the dissection which it represents were prepared by Mr. G. R. Brook at one time in the Museum's exhibition section. The scale model of the head of a Right Whale (fig. 9) was constructed by Mr. D. Macer-Wright.

Most of the material used for the dissections was obtained by an arrangement under which stranded cetaceans, the property of the Crown as Fishes Royal, are forwarded to the Museum if required. Thanks are expressed to the Receivers of Wreck and Coastguards for their continuing help in this direction.

Mr. P. E. Purves assisted Mr. Burne prior to the war and was subsequently responsible for arranging the display of the specimens, diagrams and labels according to the prepared plan. His participation in the work is duly acknowledged and also his close collaboration with the writer of the handbook in the work connected with the description of the eustachian sacs referred to in the text.

Acknowledgment is made to Professor F. J. Cole, Drs. Remington Kellogg, N. A. Mackintosh, L. H. Matthews, D. A. Parry, G. G. Simpson, G. L. Walls and Professor R. Walmsley for permission to quote from their writings, and also to the following publishers who have generously given their permission for extracts to be made from books published by them :— Messrs. A. & C. Black Ltd., London, John Murray, London, Macmillan & Co. Ltd., London, Charles C. Thomas, Springfield, Illinois, the Editor, Hvalrådets Skrifter, Oslo, and the Director, Cranbrook Institute of Science, Michigan. The names of the authors and the titles of the books concerned are detailed in the bibliography on page 66.

The handbook has been written by Dr. F. C. Fraser who wishes to express his sincere thanks to Professor A. J. E. Cave, Department of Anatomy, St. Bartholomew's Hospital, for his most generous assistance and helpful criticism during the preparation of the manuscript.

H. W. PARKER,
Keeper of Zoology.

BRITISH MUSEUM (Natural History),
LONDON, S.W.7.
November, 1951.

INTRODUCTORY

THE order Cetacea includes those animals popularly referred to as Whales, Dolphins and Porpoises. It is divided into three sub-orders, viz.: the Archaeoceti or Zeuglodonts, known as fossils only, the Odontoceti or toothed cetaceans and the Mysticeti, the baleen, or whalebone whales. The earliest known Archeocetes are of Eocene age and none has been discovered later than the Oligocene period. The latter period contains the oldest known relatives of existing Odontocetes and Mysticetes which, however, are not prominently represented as fossils until the Miocene. The earliest known cetaceans are already distinguishable either as toothed or as whalebone whales; they give little indication of their relationships with other mammals and, indeed, so obscure are the affinities of the order that Simpson (1945) says: "It is clear that the Cetacea are extremely ancient as such and that none of the various proposals of exact source, such as that deriving them from certain Creodonts*, is very probable. They probably arose very early and from a relatively undifferentiated eutherian ancestral stock." (Some tentative evidence touching the zoological affinities of the Cetacea would perhaps suggest their remote kinship with the Artiodactyla or even-toed Ungulates.)

* A fossil sub-order of carnivorous mammals.

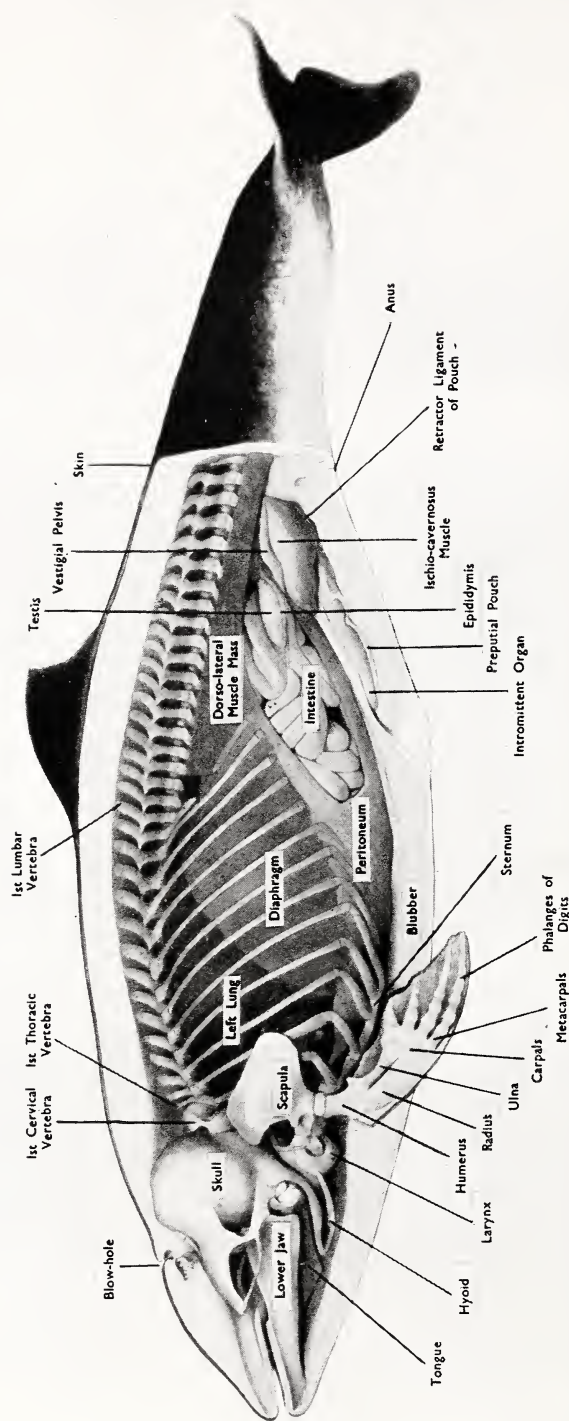


FIG. 2. Dissection of male porpoise, *Phocaena phocaena* with the soft tissues of the left side of the head and body wall removed to show the skeleton and viscera.

GENERAL STRUCTURE

The true mammalian position of the whales and dolphins in the Animal Kingdom was not acknowledged until towards the end of the seventeenth century, although Aristotle in classical times recognised the differences between the Cetacea and the fishes whose habitat they share; for all cetaceans are exclusively aquatic in their mode of life, never voluntarily coming on to dry land and soon perishing there if they cannot regain their normal aquatic environment. As mammals they are air-breathing and warm-blooded, their developing young are carried within the body of the mother for many months, and when born, and until they can fend for themselves, they are dependent on their mothers' milk for nourishment.

The superficial resemblance of cetaceans to fishes is in itself reason enough for mistakenly assuming a close relationship between the two. The cetacean body (fig. 2) is so shaped as to offer the least resistance to the animal's movement in the water. The head, which is always more or less tapered towards the tip of the snout, passes at its hinder end into the trunk without trace of any constriction definable as a neck. The trunk, from about the middle of the body-length, continues tailwards with a diminishing cross-section to the tail stock, which terminates in two laterally expanded fleshy lobes known as the flukes. The dorsal fin is an unpaired extension, similar in structure to the flukes. Most, but not all, species have this back fin; in smaller forms it is situated about the middle of the back; when present in the bigger whales it is always situated nearer to the tail, at or near the commencement of the hindmost third of the body-length.

Details of the structure of the dorsal fin and tail may be seen by reference to the dissections shown in figures 3 and 4. The dorsal fin is an extension of the skin and underlying fibrous tissue of the back, and contains neither bony support nor muscle. It is strengthened to resist lateral pressure by a layer of strong ligamentous fibres running from its base to its tip close beneath the skin. Its central core is composed of softer fibrous tissue with its component fibres disposed at right angles to the ligamentous layer. Figure 3A shows a longitudinal section of the dorsal fin of a Common Dolphin, *Delphinus delphis*, exposing to view the fibrous core and demonstrating the complete independence of the fin from the body musculature. The

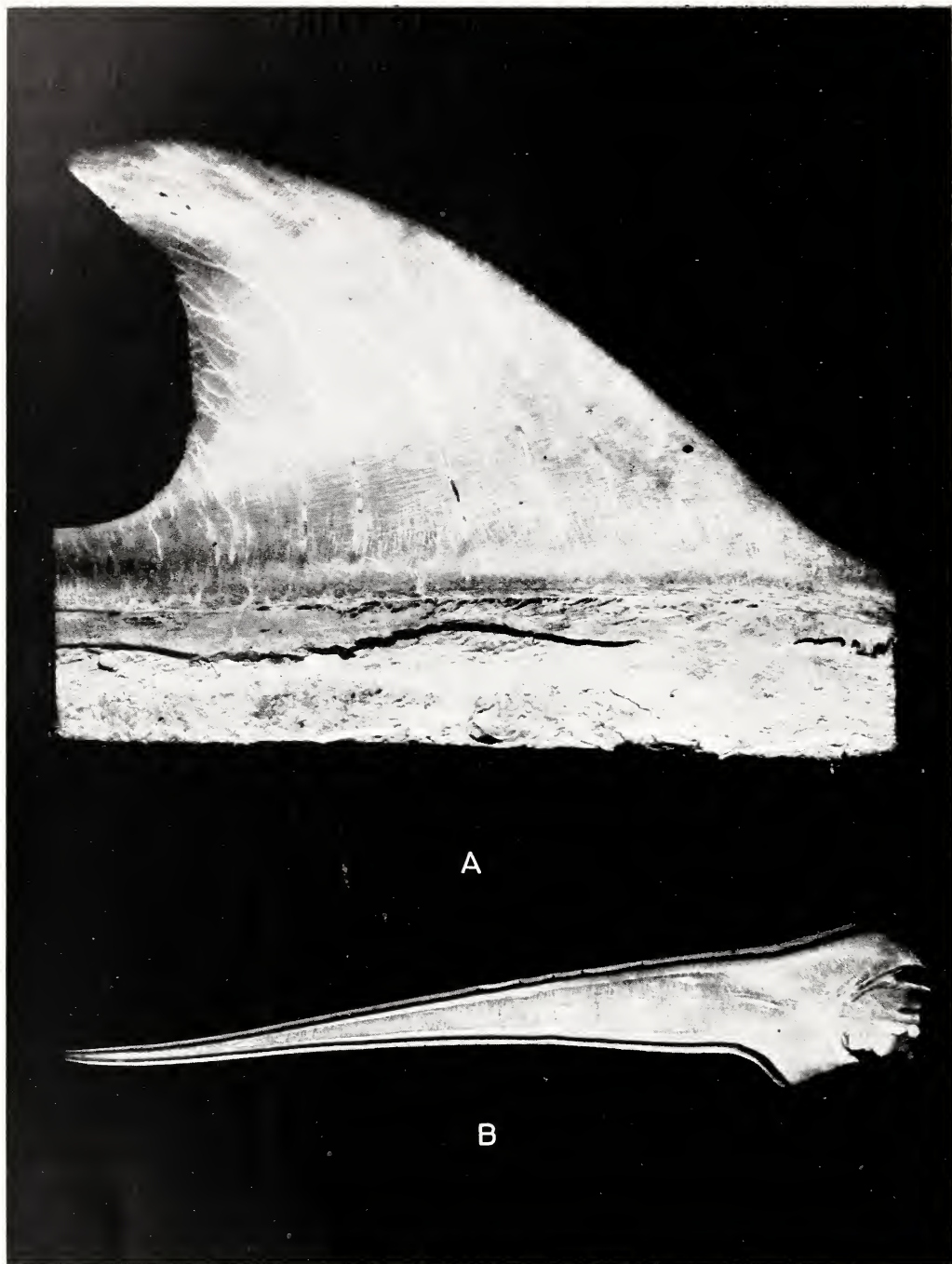


FIG. 3. Structure of dorsal fin of Cetacea.

- A. Dorsal fin of a Common Dolphin, *Delphinus delphis*, in longitudinal section.
B. Dorsal fin of a White-beaked Dolphin, *Lagenorhynchus albirostris*, in transverse vertical section.

transverse section of the back fin of a White-beaked Dolphin (fig. 3B) shows both its strengthening superficial layer of ligamentous fibres and its softer fibrous core.

The tail is the principal organ of locomotion. The left and the right flukes lack any bony support save for the backbone which lies between them. The movement of the tail is mainly up and down and is effected by the contraction of the great trunk muscles whose tendons are attached to the extremity of the backbone. The tail of a White-beaked Dolphin, *Lagenorhynchus albirostris* (fig. 4A), dissected to show the general structure and the relation of the flukes to the backbone, demonstrates also (on the left side, from which the skin alone has been removed) the superficial ligamentous layer of the tail, whilst on the right side this layer also has been dissected away exposing the inner fibrous core. A section from front to back through one of the flukes of a Common Porpoise, *Phocaena phocaena* (fig. 4B), shows the streamlined contour of this appendage: the transverse section through the tail of a Common Dolphin (fig. 4C) shows the centrally placed vertebra, the tendons lying just external thereto and the more distantly placed blood-vessels, as well as the features of the ligamentous layer and the soft core as displayed in the two associated specimens.

The cetacean forelimbs are fin-like in external appearance and are usually referred to as flippers. The term paddles, sometimes used, is open to the objection that it implies a propelling function which these limbs do not possess. Anatomically they have, however, the same fundamental structure as the fore-legs of a terrestrial mammal, though greatly modified for use in water. The typical features of the limb are shown in the dissection of a right flipper of a 12-ft. long foetal Blue Whale, *Balaenoptera musculus* (fig. 5), and also in the general dissection of a Porpoise (fig. 2). In both specimens the outer surface of the flipper has been removed to show the relative position and dimensions of the contained skeleton. The porpoise fore-limb is associated with its shoulder blade (scapula). This is broad, flattened and fan-shaped, with an acromion process originating near the anterior border of the scapular body and directed forwards as a flattened, tongue-like projection, and with a coracoid process, similarly directed, below this. The Right Whales have a greatly reduced coracoid, and the Humpback Whale

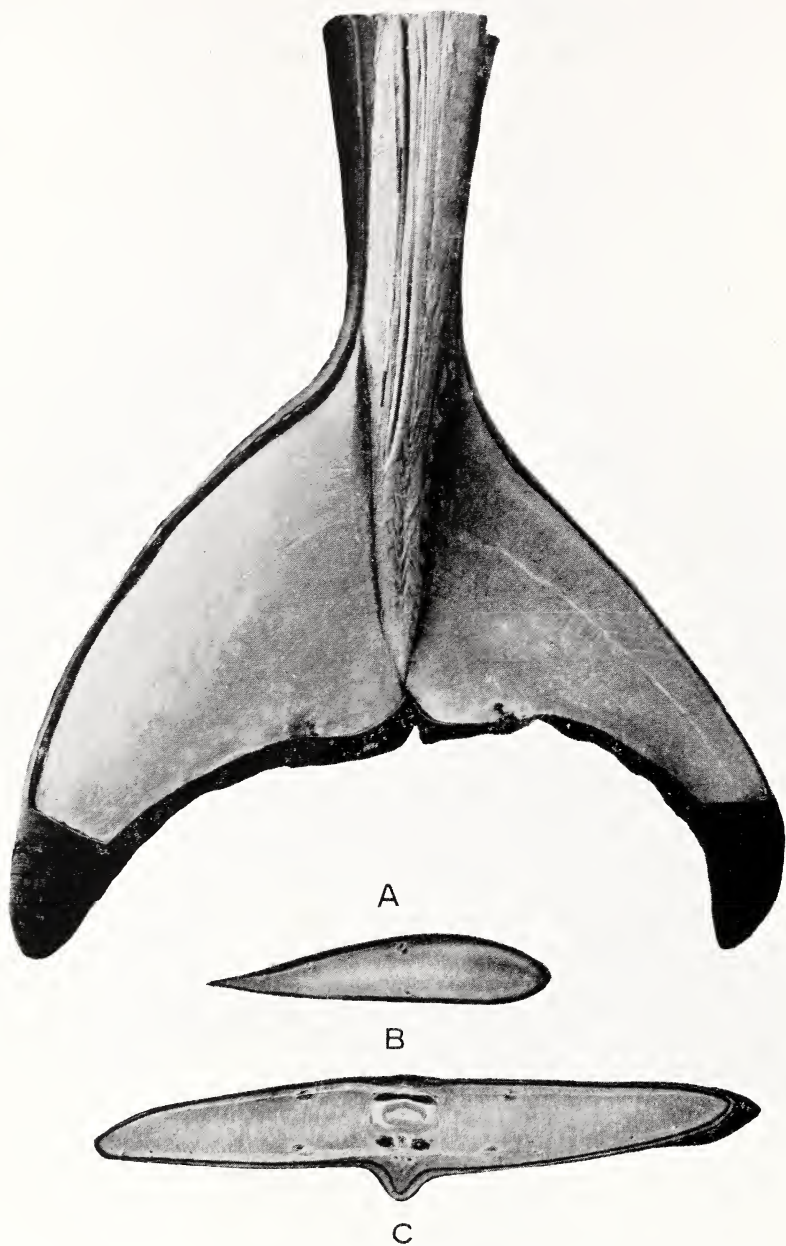


FIG. 4. Structure of the tail.

- A. Tail of a White-beaked Dolphin, *Lagenorhynchus albirostris*. The superficial ligamentous layer of the flukes is exposed on the left, the softer central fibrous core on the right.
- B. Section from front to back through the fluke of a Common Porpoise, *Phocaena phocaena*.
- C. Transverse section through the tail of a Common Dolphin, *Delphinus delphis*.

lacks both acromion and coracoid processes. A collar-bone (clavicle) is wanting in all cetaceans.

The Blue Whale flipper is long, narrow and flattened, and all the fingers (digits) are enclosed together within the common integument of the limb. The upper arm-bone (humerus) is relatively short; its head, which articulates with the shoulder blade, is large and globular: towards its lower (distal) end the bone becomes somewhat flattened and terminates in two facets to which the upper (proximal) ends of the two fore-arm bones (ulna and radius) are applied. These fore-arm bones are short, much flattened and parallelly disposed. The upper (proximal) end of the ulna (olecranon), cartilaginous in the specimen displayed, is distinguishable as a flattened, hatchet-edged protuberance on the margin of the flipper at the proximal end of the fore-arm. The joint (elbow joint) between the upper arm and the fore-arm permits scarcely any motion and in old animals there is often here complete fusion of the two segments of the forelimb. The wrist bones (carpalia), also entirely cartilaginous in the Blue Whale limb exhibited but replaced by bone to a greater or lesser extent in the adult, form a mosaic between the fore-arm bones and the bones of the palm of the hand (metacarpalia). The metacarpals are indistinguishable in shape from the adjacent, more distally-situated, phalangeal (finger) bones. The whole hand is very much elongated, mainly by reason of the large number of phalanges, and in the Blue Whale amongst others it is narrowed by absence of the first digit (pollex). The phalanges are provided at each end with a block of cartilage (epiphysial cartilage): as the animal grows older this cartilage is partially replaced by bone which fuses with the appropriate phalangeal shaft, but even in the adult animal a mass of cartilage separates one phalanx from the next. In the Right Whales and in all the Toothed Whales the full primitive mammalian number of five digits persists. In the latter group there is variation from species to species in the length, breadth and general shape of the flipper and in the number of phalangeal bones present.

Cetaceans have no external trace of hind limbs. But in the body-wall, about the position where in land mammals the hind-limb skeleton makes contact with the backbone, there is situated a pair of bony pelvic vestiges. A sacrum is wanting in all known cetaceans and the vestigial pelvic bones present have completely lost all contact with the vertebral column. The

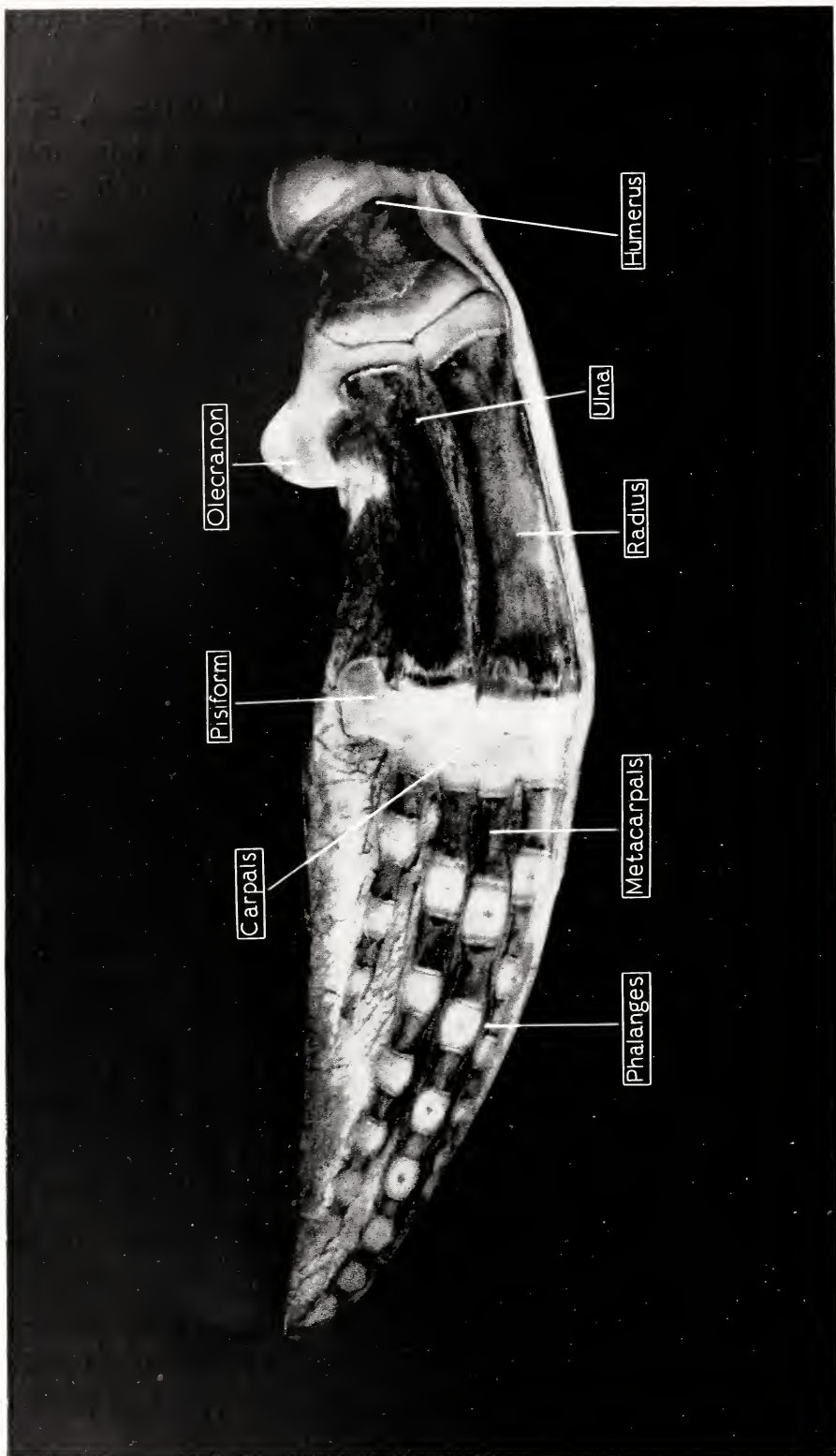


FIG. 5. Right flipper of a foetal Blue Whale, *Balaenoptera musculus*, with the soft tissues removed from the outer surface.

extent to which the thigh-bone (femur) and the shin-bone (tibia) elements are represented is variable both as regards different genera and different individuals. With the exception of the Sperm Whale, which may possess a femoral vestige, the Toothed Whales lack these hind-leg bones. Among the Baleen Whales, the Right Whales show the least reduced condition, viz.: a bony femoral vestige and what has been interpreted as a cartilaginous tibia. In the Rorquals an occasionally present cartilaginous mass associated with the pelvic bone is said to represent the femur.

Portions of the axial skeleton (skull, backbone, ribs, etc.) are exposed in the dissection of an entire Porpoise (fig. 2) and attention may be drawn to certain characteristic anatomical features thereof. The cranial portion of the skull is strongly compressed from front to back and is globular in appearance: the facial portion is produced in the form of a rostrum, commonly referred to as the beak. The seven cervical vertebrae are greatly compressed and therefore constitute a very minor component only of the total backbone length: the degree to which they fuse mutually varies considerably. In the Gangetic and the South American River Dolphins, and in the White Whale and the Narwhal, all seven cervical elements are normally free. This too is usually the condition in the Rorquals among the Baleen Whales, whereas in the Right Whales all seven cervical vertebrae are fused into one osseous unit. The Toothed Whales (other than those just mentioned) have the first two cervicals (atlas and axis) fused, with, usually, some of the hinder cervicals united to these: but in the Sperm Whale the atlas is separate and the remaining six cervical vertebrae are fused into a composite bony mass. The Bottlenosed Whale resembles the Right Whales in that all its seven cervical vertebrae form by confluence a single unit.

In the vertebrae behind the cervicals, transverse processes are well developed, especially in the loin (lumbar) and tail (caudal) regions, but like the neural spines of these same vertebrae they progressively diminish in size and finally disappear towards the tail-tip. In the tail region occur the chevron bones, ventral V-shaped elements faceted to the under surfaces of contiguous vertebral bodies, in such fashion that a given chevron bone articulates simultaneously with the hinder end of one vertebra and the fore-end of the vertebra next following.



FIG. 6. Strip of skin from the chin of a Blue Whale, *Balaenoptera musculus*, showing four slender hairs.

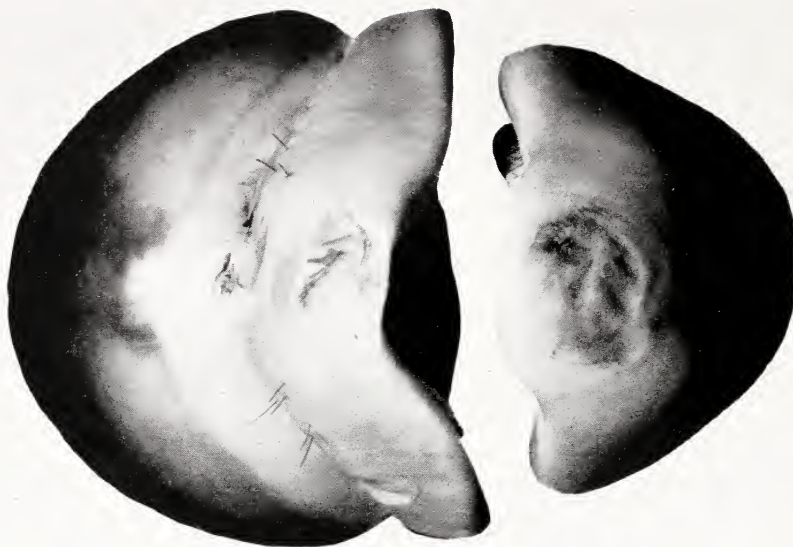


FIG. 7. Snout of a White-beaked Dolphin, *Lagenorhynchus albirostris* with asymmetrically disposed bristles.

The number of ribs varies according to the different species, some twelve to sixteen pairs being usual. The Southern Bottlenosed Whale with but eight pairs of ribs is unique in possessing fewer ribs than any other mammal.

The breast-bone (sternum) of the Toothed Whales is composed of several bony elements which fuse to form a single elongated unit, to which a varying number of sternal ribs may be attached. The breast-bone of the Whalebone Whales, however, is so greatly reduced in size that it provides attachment for the first pair of ribs only.

INTEGUMENT

Although whales are mammals they have almost completely lost the hairy body covering which is otherwise so characteristic of the class. The skin is devoid of sweat glands (and possibly sebaceous glands also) and it has attained a polished exterior smoothness unmatched by that of any other mammal. The hairs that remain are few in number and are restricted to the head. The strip of skin from a Blue Whale shown in figure 6 was taken from the chin where in Rorquals there is a sparse "beard" composed of between twenty and forty hairs arranged in two vertical rows (Mackintosh and Wheeler, 1929). Along each mandible and on the surface of the snout, hairs are also to be found both in foetal and in adult animals. In certain of the toothed cetaceans on the other hand, for instance in the Narwhal, *Monodon monoceros*, and the White Whale, *Delphinapterus leucas*, according to Brazier Howell (1930) hairs are not present at any stage of development. Other Odontocetes, for example the White-beaked Dolphin, *Lagenorhynchus albirostris* (fig. 7), display a few small bristles or hairs on the side of the snout. These are to be seen in foetal and some very young animals but have disappeared in the adult.

A very characteristic feature of all cetaceans is the subcutaneous envelope of fat (blubber) which invests the body. Figure 8 shows two sections of blubber from a Sei Whale or Rudolph's Rorqual, *Balaenoptera borealis*. The upper specimen is from the grooved throat region and the lower is from the side of the body. The outermost layer of the skin (stratum corneum) is extremely thin and is so delicate in structure that it can be peeled off a freshly-dead animal without difficulty. Beneath this some authors, though

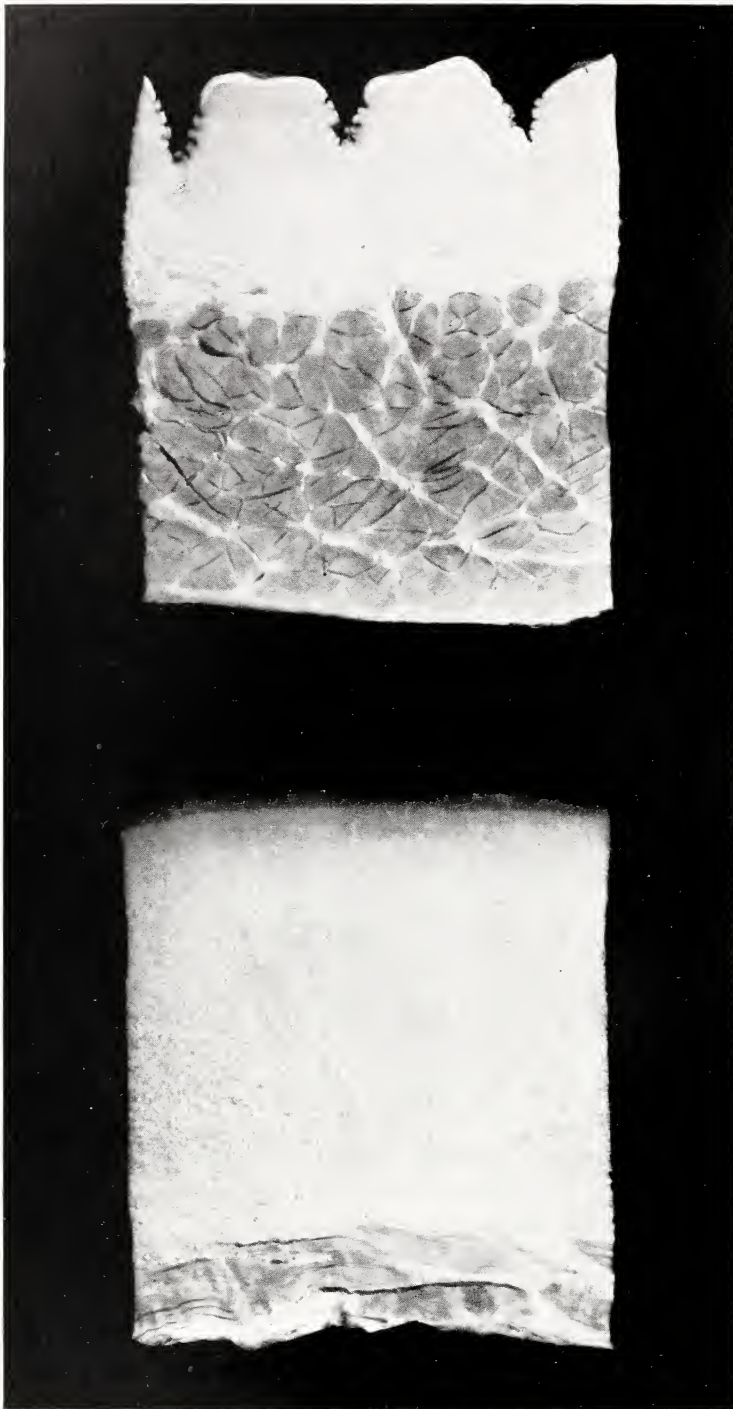


FIG. 8. Two sections of blubber taken respectively from the throat (upper specimen) and from the neck of a Sei Whale or Rudolphi's Rorqual, *Balaenoptera borealis*.

not all, recognize an even thinner layer (*stratum lucidum*). Next internally is a thick layer (*stratum germinativum*), into which project the exceptionally long papillae of the dermis. This last, on its deep aspect, merges into the hypodermis, the blubber layer in the restricted sense. This blubber layer is, in comparison with those external to it, of immense thickness, and is made up of fat cells interspersed with tough fibrous tissue. Brazier Howell (*loc. cit.*) suggests that the blubber layer may in fact be a true component of the dermis, since it differs so greatly from the simple layer of soft subcutaneous fat found in seals.

Blubber is generally regarded as functioning both as a food reserve and as an insulator. Whales which have been for a period in high polar latitudes where food is abundant acquire a great thickness of blubber, whereas those taken in tropical waters have the fat layer much reduced because food is scarce there and the fat reserve has to be drawn upon to supply the needs of the body. However, with regard to the conventionally accepted theory of the insulating function of blubber, Parry (1949) has recently shown that the conductivity of this layer is such that whales "lose heat at a greater rate than the basal metabolic rate of land homotherms (warm-blooded animals), even when the blood-flow through the blubber is negligible." He suggests that whales need to maintain swimming activity in order to remain warm.

BALEEN OR WHALEBONE

The group of whales called *Mysticeti*, that is Baleen or Whalebone Whales, is so named because its included species are characterized by the possession within the mouth of a system of horny plates so arranged that they act as a sieve to strain from the entrant sea-water the small marine creatures which form the whale's food. A model of the head of a Right Whale, wherein the right lip and part of the baleen on the right side is cut away, demonstrates the arrangement of the baleen plates in the mouth (fig. 9). These plates are in two series, or "sides," suspended from the upper jaw. The outline of each plate is roughly that of an elongated triangle with the shortest side attached to the palate at right angles to the long axis of the head: the outer (lateral) edge of the plate is smooth (fig. 10); and the inner (medial) boundary is frayed out into a fringe of bristles (fig. 11).



FIG. 9. Model of the head of a Right Whale with the right lower lip and part of the baleen on the right side cut away to show the arrangement of baleen plates in the mouth.

The plates are spaced one behind the other at distances of about a quarter of an inch and their fringes combine to form a matted straining device. One or more smaller, narrower, accessory plates may be present medial to the main plates, but any such differ structurally in no way from the latter. A “ side ” of baleen may consist of upwards of three hundred plates.

The size, shape, colour and quality of the baleen varies according to the kind of whale concerned and these features are used as a means of distinguishing the several species. The Rorquals have shorter, broader, coarser and less flexible baleen, whilst that of the Right Whales is longer (up to 12 feet), narrower, of finer quality and much more flexible (fig. 12).

The origin of baleen is similar to that of the hair of mammals. It is an epidermal product, that is to say it originates from the skin. A diagram of its structure is shown in figure 13. The growing baleen is moulded in the skin on a mass of underlying connective tissue, the dermal process, which is differentiated into a basal plate and long tapering papillae. In the skin or epidermis external to the papillae the horn tubes are formed and it is the free ends of these which make the baleen fringe. The epidermis external to the basal plate produces:—

- (1) the compacting horn between the horn tubes;
- (2) the covering layer of horn which envelops the compacting horn and the horn-tubes except at the free ends of the latter; and
- (3) the intermediate substance which is a cushion of softer horn between adjacent plates.

Preparations of developing baleen from a 20-foot foetal Blue Whale are shown in figure 14. During foetal life the skin of the mouth and the underlying flesh thicken along the margin of the upper jaw to form a swelling marked on the surface by diagonal rows of conical processes (D). These processes, starting from the outer margin of the swollen band, rearrange themselves and fuse to form transverse plates which are the forerunners of the baleen plates of the adult (C and E). The mass of growing skin is based upon underlying plates of connective tissue fringed by the thin papillae (A, E). The skin surrounding the papillae, as already described, extends between and around the horn tubes, compacting and covering them with a horny investment. The skin between the basal plates forms the soft horny anchoring intermediate substance.

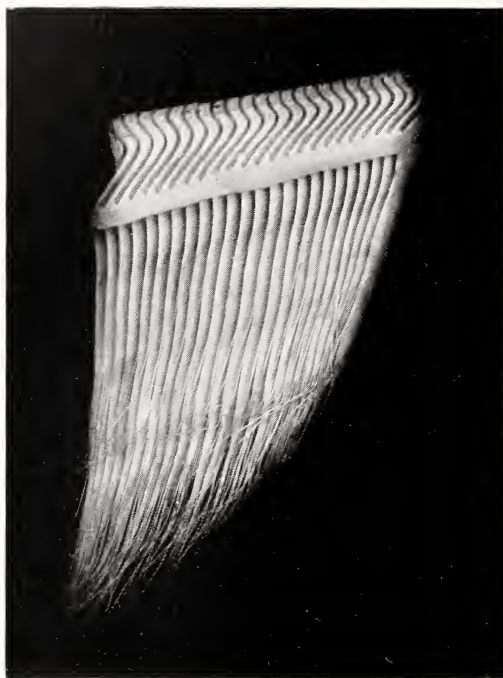


FIG. 10. Part of a "side" of baleen, to show the smooth outer edges of the plates.

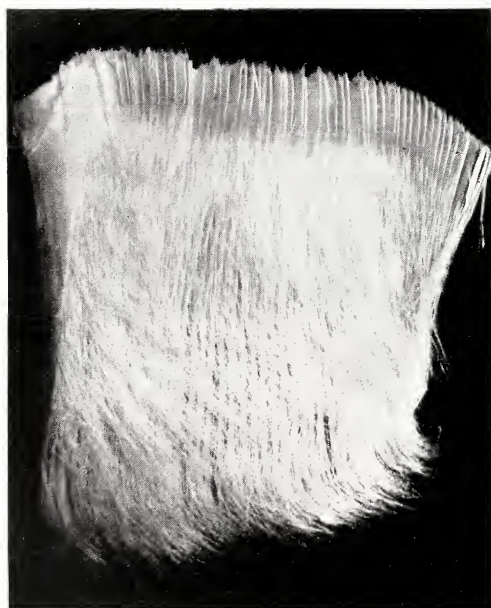


FIG. 11. Part of a "side" of baleen to show the frayed inner edges of the plates.

HEAD

It was mentioned above that the Right Whales differ from the Rorquals in having much longer and more flexible baleen; correlated with this and with methods of obtaining food are certain other distinctive features in the anatomy of the head in the two families. Thus in the Right Whales the upper jaw is pronouncedly bowed so that it is separated from the lower jaw-bones at the summit of its arch by a distance of some feet. The lower lip forms two arcuate crests, one on each side, resting on the lower jaw-bones and fitting into the arch of the upper jaw. At the chin the edge of the lower lip is but little above the underlying jaw-bones. The shape of the lower jaw as a whole has the appearance of a gigantic scoop and it is probably in a scoop-like manner that it functions when the whale is catching the shoals of small marine animals on which it feeds. The tongue is prominent and muscular and is undoubtedly employed for collecting the food from the inner sides of the baleen plates whereon it is left when the water taken into the mouth along with it has drained to the exterior.

In the Rorquals, however, the fore part of the head is much flatter and broader than in the Right Whales, the edge of the upper jaw lying for most of its distance on each side nearly parallel to the lower lip. The baleen is short and the tongue a flaccid mass which can play no very active part in food collection. But the Rorquals, unlike the Right Whales in which the under surface of the body tailwards of the chin is smooth, have the throat region scored externally with numerous longitudinal grooves, extending from the lower edge of the lower jaw almost to the navel and laterally for a considerable distance up on to each side of the body. A cross section of this grooved region is shown in figure 8. The disposition of the muscles immediately deep to the grooves, and the extension of the skin of the throat region (which is evident in dead Rorquals), suggest the probable method of feeding in this group. When the whale is about to feed it is believed that the mouth is opened slightly and the muscles under the skin of the throat are relaxed, so that a large cavity is formed above the floor of the mouth into which water and whale food flow: the mouth is then closed, the muscles under the throat grooves contract, and the water in the mouth is thus forced to the exterior between the baleen plates, leaving the concentration of whale food on the inner fringes of these blades.



FIG. 12. Plates of baleen from a Right Whale (left) and a Rorqual (right), with 1-foot scale.

TEETH

The dissection of a Common Porpoise (fig. 2) shows the arrangement of teeth in one of the Odontoceti or Toothed Whales. The disposition of the teeth and the uniformity of their shape are typical of many members of the group, the Porpoises alone being peculiar in having the tooth-crowns chisel-shaped. None of the recent cetaceans has its teeth differentiated into incisors, canines and cheek teeth. The teeth on each side of both the upper and the lower jaw are peg-like, single-rooted structures and no cetacean is known to develop more than one functional set. The Bottlenosed Dolphins, *Tursiops* spp., possess about the same number of teeth as the Common Porpoise (i.e., 21–24 in each row), though of larger size, whereas the Common Dolphin and its relatives have teeth of similar diameter to those of the Porpoise, but in them each row is composed of from 40–65 teeth, or up to more than 240 in all. The Killer, the Pilot Whale and the False Killer, all of them large sized Dolphins, possess from 7–12 stout teeth on each side of the upper and the lower jaws, while Risso's Dolphin, which is nearly related to the Pilot Whales, has from two to six teeth in each row in the lower jaw but none in the upper. In the male Narwhal the only obvious tooth is a spirally marked tusk projecting forwards from the upper jaw to a distance sometimes of eight feet. The apparently toothless female Narwhal has two small functionless teeth embedded in the bones of the snout.

Male Beaked or Bottlenosed Whales have usually a pair (sometimes two pairs) of teeth in the lower jaw, the shape and position of which, according to the species concerned, may vary considerably. Females of this family are apparently toothless although equipped with non-functional teeth which never penetrate the gums. In several species minute vestigial teeth have been found in upper and lower jaws.

The Sperm Whale has two rows, each of about 24 teeth, in the lower jaw, but only a few vestigial teeth in the upper jaw.

Finally, with regard to teeth it should be noted that whilst the distinction between the two main sub-orders of recent cetaceans is based on the presence or absence of teeth or of whalebone, even the Whalebone Whales possess vestigial teeth during foetal life. These are embedded in the gums and are resorbed as the baleen begins to develop, all trace of them being lost by the time the calf is born.

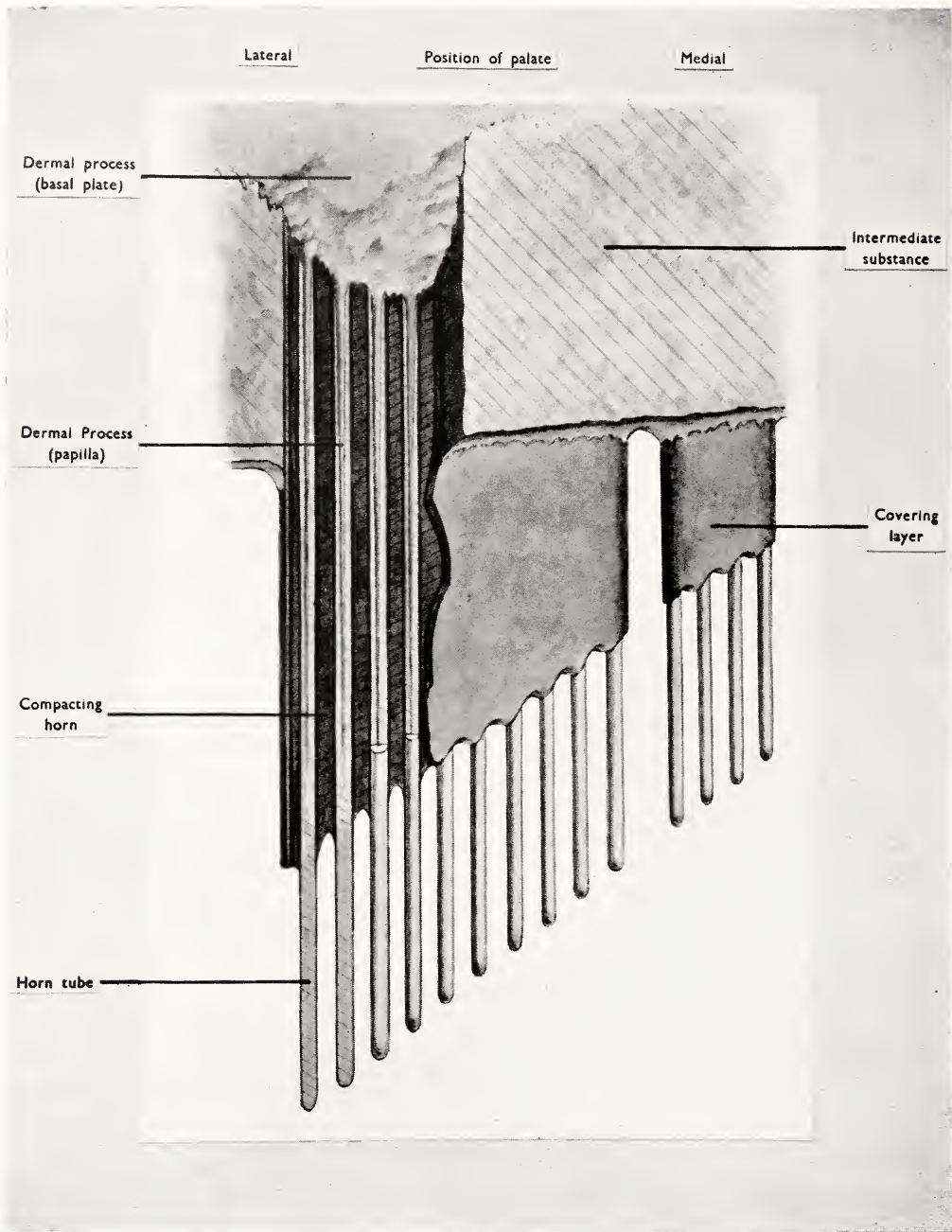


FIG. 13. Diagram of the structure of baleen.

ALIMENTARY SYSTEM

The anterior end of the alimentary canal of a Common Porpoise is shown in the dissection represented in figure 1. The lips bounding the mouth aperture are immobile, the opening and closing of the mouth being therefore entirely dependent upon the movement of the lower jaw in relation to the upper. In the Toothed Whales the tongue is mobile as in the generality of mammals; its condition in the Whalebone Whales has already been referred to.

The mouth cavity at its hinder end passes into the pharynx, from the floor of which the upper end of the larynx projects, to traverse the food passage and to link up with the hinder end of the nasal cavity (see also fig. 20), above the roof of the pharynx. The food channel thus passes on either side of the elevated larynx and continues into the oesophagus, a simple cuticle-lined tube (see also figs. 27 and 30), which opens posteriorly into the first stomach. It may be well here to quote Brazier Howell (1930) on the size of the cetacean throat. "The oesophagus of the Odontoceti may be said to be of normal size, but that of the Mysticeti is remarkable for its small diameter. That of a Finback of 70 feet was not larger than five inches at the most."

The first stomach of the Porpoise is lined with cuticle continuous with that of the oesophagus and may therefore be regarded simply as a special crop-like dilatation of that tube. Although its walls are devoid of digestive glands, "its contents," according to Flower and Lydekker (1891), "undergo partial digestion probably caused by the regurgitation into it of the secretion of the second, or true digestive compartment." This second stomach communicates with the first near the latter's oesophageal end: compared with the first stomach it is smaller and has much thicker, plicated, and glandular walls. It communicates by a small opening near its tailward end with a pyloric compartment (not visible in the given figure (fig. 1) of the dissection), which is contorted and is subdivided by a constriction into a smaller globular portion next to the second stomach and an elongated distal portion continuing to the pylorus. Beyond the pylorus the first part of the small intestine (duodenum) is likewise a dilated saccular cavity, into which opens the common excretory duct from the liver and pancreas. The liver is a relatively simple, bilobed mass lying at the anterior end of the belly (peritoneal) cavity

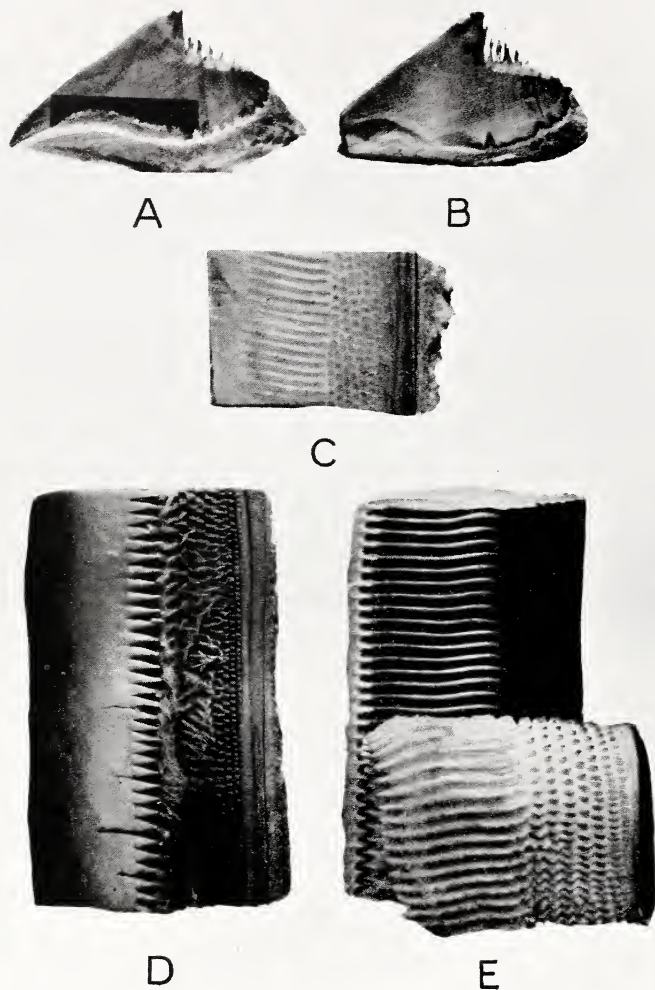


FIG. 14. Developing baleen from a 25-foot long foetal Blue Whale, *Balaenoptera musculus*.

A and E. Preparations to show dermal processes (basal plates and papillae).

B. Plate of developing baleen.

C. Developing baleen plates and conical processes cut transversely.

D. Rows of conical processes which fuse together in transverse lines to form the baleen plates.

immediately behind the diaphragm and in close apposition to the stomachs and the duodenum. A gall-bladder is wanting in all cetaceans. The pancreas, obscured in the figured dissection by a prominent sheet of peritoneum (omentum) lies in a space between the first stomach and the duodenum. The spleen, again not visible in the dissection as displayed, lies on the right side of the first stomach. The duodenum continues into the remainder of the small intestine, a portion of which is shown in the dissection. The situation of the terminal portion of the large intestine (rectum) in relation to adjacent viscera is shown in the dissection represented by figures 32 and 33.

The stomach of Whalebone Whales is compartmented in a similar way to that of the Porpoise just described, whereas in the Bottlenosed Whales according to Beddard (1900), "nine, ten, even thirteen or fourteen divisions have been recorded."

RESPIRATORY SYSTEM

Being mammals, cetaceans obtain their supply of oxygen by receiving air into the lungs in a manner identical with that of the terrestrial members of their class. But they differ from land mammals in their conspicuously irregular periodicity of breathing. This is correlated with a habit of life which demands that relatively long periods be spent below the surface of the water, during which air for the replenishment of the lungs is not available. Thus the normal respiratory sequence of a cetacean is a succession of inspirations and expirations with relatively short intervals between successive respiratory excursions, followed by a much longer period wherein the animal remains submerged with its lungs charged with air. Each of these periods can vary greatly according to the kind of cetacean and to the immediate individual circumstances, i.e., whether the animal be feeding, migrating, resting or hunted. In passing it may be noted that the breathing out, the "blow," of a whale does not consist of a fountain of water as erroneously depicted in so many old whaling prints. It consists of the expired air, laden with water-vapour, which, on contact with the colder external atmosphere, condenses and so becomes visible. Thus the "blow" is more conspicuous in high (cold) latitudes than in warmer tropical regions, and more obvious in the bigger than in the smaller members of the order.



FIG. 15. Cast of the nostrils of a Sei Whale, *Balaenoptera borealis*, in their closed position.



FIG. 16. Blowhole of a White-beaked Dolphin, *Lagenorhynchus albirostris*.

The various specializations of the respiratory system of cetaceans are correlated with their adoption of a permanently aquatic habit of life. The nostrils (or blowholes) are, with one or two exceptions to be mentioned, in a position on the head far removed from the front end of the snout. They have become transferred to the top of the head (fig. 2) and are so situated there that when the animal breaks surface the external opening of the air passage from the lungs is the first part of the head to be exposed. This transference has profoundly affected the architecture of the skull, particularly in its front portion. The nasal bones, from being the roofing elements of the nasal cavity of the typical land mammal, have become reduced to blunt, wedge-shaped blocks in the Whalebone Whales, and to mere nodular vestiges in the Dolphins. The multiple, complicated turbinal bones, which almost fill the nasal cavity of the land mammal, have disappeared. The bones of the upper jaw (the maxillae and premaxillae) extend far in front of the nostrils to form a "beak" or rostrum.

The blowhole of Whalebone Whales is a paired structure (fig. 15) consisting of two long, narrow slits which, when closed, make a forwardly-directed acute angle from which a median groove extends tailwards between and for roughly the same distance as the slits. The latter are controlled by a muscular mechanism which enables them to open and close as required. Dilation of the nostrils is accompanied by marked elevation of their anterior margins, thus providing a barrier against the entry of water when the animal is in motion on the surface.

The passages leading from the nostrils are of simple structure in the Whalebone Whales as compared with those of the Toothed Whales. Brazier Howell (loc. cit.) states, "By manual investigation within the passages of a fresh adult [Whalebone Whale] I could not discover any true diverticula but only a slight folding and wrinkling of the mucosa rostrad and to a lesser extent laterad. Schulte considered the arrangement of this to be such as to aid closure when pressure is supplied from without."

Before passing to the condition of the nostril (narial) passages in the Toothed Whales it should be noted that in this sub-order the blowhole is a single aperture, usually crescentic in shape with the concavity of the crescent towards the snout (fig. 16). The Sperm Whale and its congener the Pigmy Sperm Whale are exceptions to this generalization, the former having a

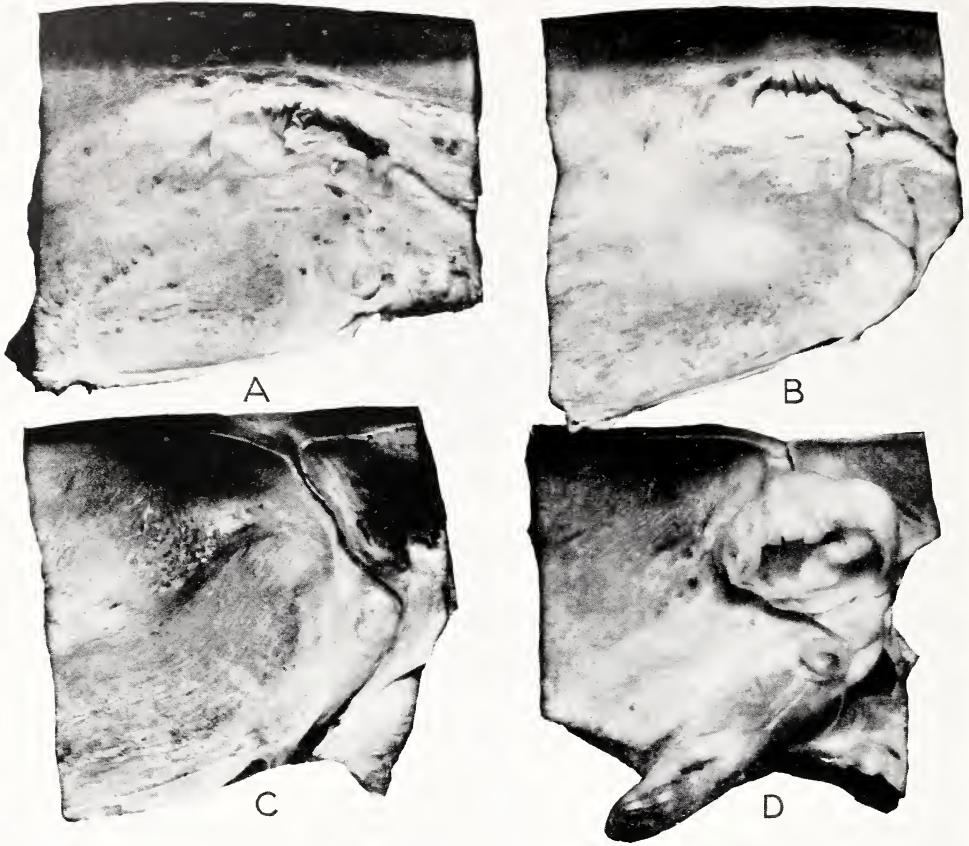


FIG. 17. Three vertical sections of the right side and a dissection of the left side of the blowhole of a Common Dolphin, *Delphinus delphis*.

- A. Section furthest from the mid line through the centre of the vestibular sac showing its pleated epithelial lining and the soft vascular tissue which surrounds it.
- B. Section nearer the mid line showing the portion of the air passage which connects the vestibular sac to the main air vent and the tongue like process which crosses it.
- C. Section through the mid line showing the backward projecting boss the surface of which is contoured to that of the posterior wall of the air passage in a close, valve like fit.
- D. Dissection showing the shape and interrelationship of the vestibular, premaxillary and subsidiary sacs which surround the nostril.

single, drawn-out S-shaped slit situated at the front of the head on the left side of the middle line, whereas the position of the blowhole in the Pigmy Sperm Whale is much as in the dolphins generally, i.e., on the top of the head, but again asymmetrically placed. It is in the form of a very flattened crescent, extending on the left side of the mid line, obliquely outwards and tailwards.

The very complicated arrangement of valves and cavities connected with the dolphin blowhole is demonstrated in the exhibit by three sections, by a dissection of the left side of the blowhole region and by two diagrams (figs. 17-19). Passing inwards from the external nasal orifice the air vent gives off two lateral diverticula, one on each side, the vestibular sacs, lined with pleated epithelium and surrounded by soft vascular tissue. Internal to the vestibular sacs the air passage is crossed by a large, downwardly projecting, tongue-like process suspended from the hinder wall of the passage. Antero-ventrally is a large posteriorly-directed boss, the surface of which is contoured adaptively to that of the posterior wall of the air passage in a close valve-like fit. Two subsidiary sacs, situated one on each side anterolaterally to the air passage, are connected therewith about the level of the apex of the boss just mentioned. Finally two large diverticula (the premaxillary sacs) extend forwards from apertures connecting them with the air passages. They lie just above the point where the air passage divides and immediately above the maxillary bones, resting upon a smooth, easily recognizable area of the dolphin skull known from its shape as the prenasal triangle.

The air passage through the skull from the superior to the inferior nares (nostrils) curves downwards round the anterior end of the brain case (see fig. 1) so that at its pharyngeal end the naso-pharynx lies above the backwardly-prolonged palatal region. The air passage next crosses the pharyngeal portion of the alimentary canal, and it is characteristic of the Cetacea, although not peculiar to them among Mammalia, that this crossing is accomplished by a special structural modification of the larynx so that a direct path is provided from blowhole to lungs and breathing is possible through the nose only (figs. 20 and 21). The lips of the pharyngeal opening of the larynx are the enlarged epiglottic and arytenoid cartilages which form an elongated spout inserted into the hinder opening of the nasal cavity and firmly held in position by the muscles of the soft palate.

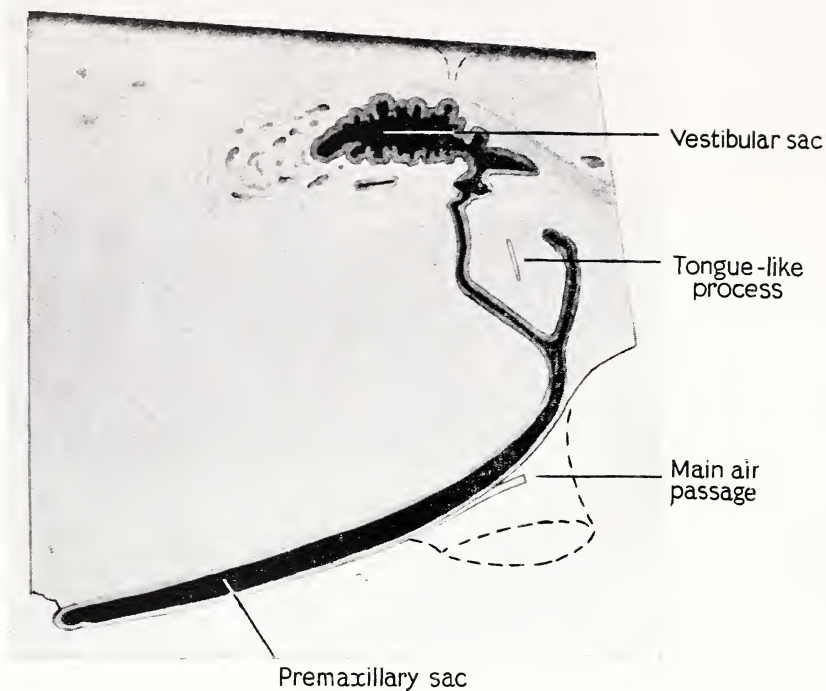


FIG. 18. Diagram of the section shown in fig. 17B.

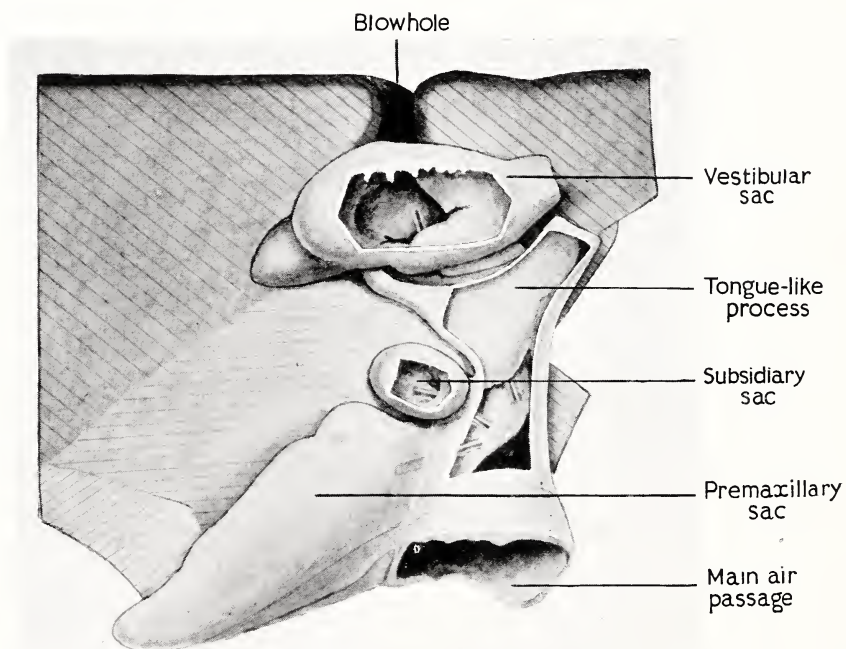


FIG. 19 Diagram of the dissection shown in fig. 17D.

The larynx is connected with the lungs (fig. 22) by the trachea with its strengthening rings of cartilage, an armature which extends not only into the bronchi but also into the smaller bronchioles which are provided with muscular sphincters.

Brazier Howell (loc. cit.) discusses the function of these cartilages and sphincters. The former, he points out, give unusual strength and incompressibility; the latter he suggests "probably close at the end of inspiration and remain so until expiration begins, preventing the gradual collapse of air spaces as outside pressure increases, thus acting in antagonism to the elastic [lung] tissue" of which there is a very great development. This pulmonary elastic tissue, according to the same authority, forms a powerful mechanism for emptying the lungs in minimal time. Otherwise, the cetacean lung possesses the features and functions of the typical mammalian organ. It is simple and non-lobulated and is contained in the chest (pleural) cavity which extends longitudinally from beneath the skull in front to the lumbar region behind, above an oblique and highly muscular diaphragm (see fig. 2).

VASCULAR SYSTEM

The system of arteries and veins in cetaceans is in the main much as in terrestrial mammals save for various specializations which will be mentioned. The heart is proportionate in size to that of land mammals. Figure 23 shows the undissected heart of a White-beaked Dolphin, *Lagenorhynchus albirostris*, viewed from behind, and figure 24 represents a dissection exposing the ventral aspect of the heart of another kind of dolphin, *Stenella euphrosyne*. The sequence in the description which follows is that of the blood coming from the veins, passing through the heart to the lungs, returning to the heart again and thence into the arterial system. Venous blood drawn from all parts of the body converges in the caval veins (inferior and right superior) shown in figures 23 and 24. In the vicinity of the opening of the inferior caval vein into the right atrium is that of the coronary sinus, the venous drainage channel from the walls of the heart itself. The contents of both caval veins are received into the relatively thin-walled right atrium and from it pass, through the right atrioventricular or tricuspid valve, into the thick-walled muscular right ventricle, regurgitation of blood into the atrium

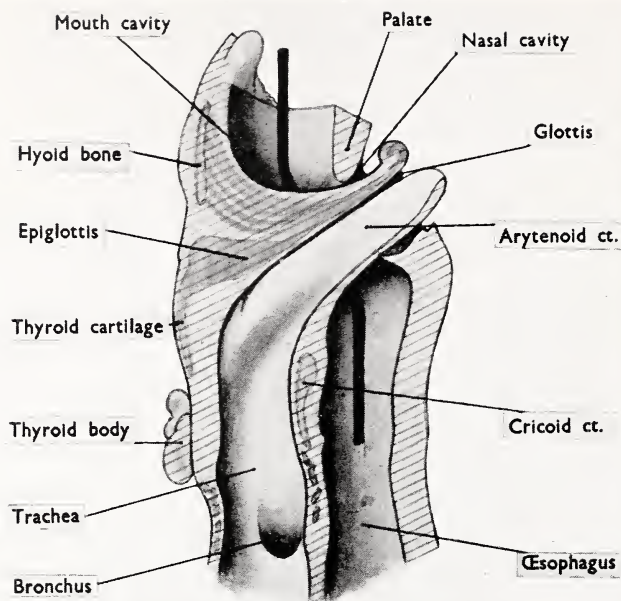


FIG. 20. Throat of a Common Dolphin, *Delphinus delphis*, in vertical section.

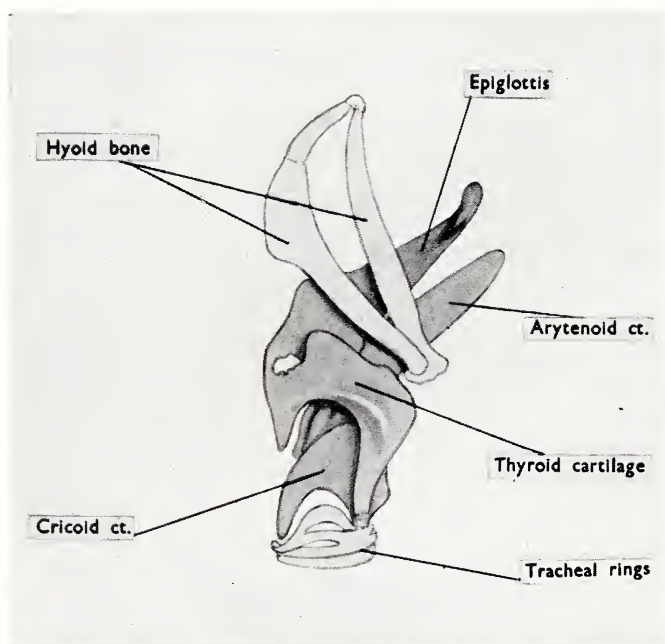


FIG. 21. Skeleton of the left half of the larynx and trachea of a Common Dolphin, *Delphinus delphis*.

being prevented by the closure of the tricuspid valve. The three cusps of this valve are controlled by the papillary muscles, being connected thereto by the slender chordae tendineae. Other muscle bundles within the ventricle are evident as fleshy columns (*columnae carnae*) projecting from the ventricular wall, while one such column, the moderator band, is attached at one end to the inter-ventricular septum and at the other to the opposite wall of the ventricle. This particular muscle band is said to prevent over-distension of the ventricular cavity. The venous blood in the right ventricle is forced by ventricular contraction into the pulmonary artery and is prevented from backflow by the pulmonary valve, composed of three semilunar cusps, situated at the junction of the pulmonary artery with the ventricle. The cusps are so arranged that the backward pressure of blood in the pulmonary artery distends them and causes their free edges to meet. The pulmonary artery (or trunk) divides into right and left branches and the venous (deoxygenated) blood in these arteries passes to the lungs where it is oxygenated, and it returns as arterial (oxygenated) blood by way of the pulmonary veins to the left atrium of the heart. The left atrium like the right is thin-walled, and the received blood passes from it through the labrio-ventricular or mitral valve into the much thicker-walled left ventricle. When this ventricle contracts regurgitation of blood into the atrium is prevented by closure of the mitral valve, whose two cusps are likewise controlled by papillary muscles and chordae tendineae. The blood forced from the left ventricle passes into the aorta and so by the systemic arteries to all parts of the body.

Before birth, while the lungs are inactive, the separation of the two functional sides of the heart is incomplete, communication taking place, as in the White-beaked Dolphin heart exhibited (and indeed as in the Mammalia generally) through an aperture (*foramen ovale*) in the partition between the two atria (see fig. 23). Blood coming to the right side of the heart is for the most part passed through this aperture into the “left heart” and thence into the aorta and systemic arteries, thus by-passing the pulmonary arteries and the lungs. This blood comprises: (1) pure arterial blood carried by the umbilical vein from the placenta, (2) impure blood from the body generally, reaching the right atrium *via* the systemic veins and the *venae cavae*.

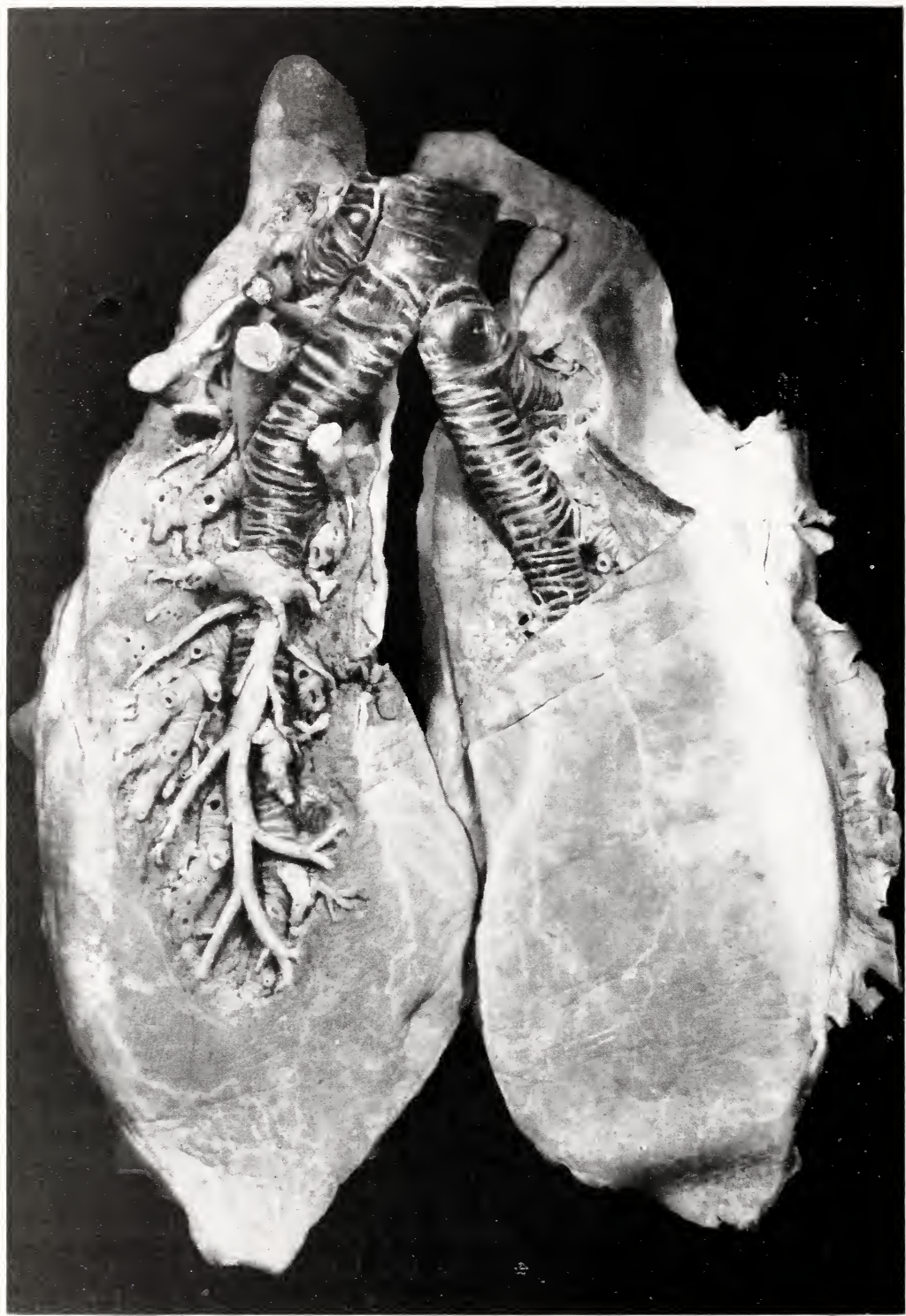


FIG. 22. Lungs of a Dolphin, *Stenella euprosyne*.

Despite the presence of the inter-atrial aperture (foramen ovale) some blood from the right atrium enters the corresponding ventricle and is passed into the pulmonary trunk: it would inevitably and disastrously reach the non-functioning lungs were it not for the presence of another by-pass between the main pulmonary artery and the systemic aorta. This is the ductus arteriosus, a short but wide arterial channel uniting the summit of the main pulmonary artery to the under aspect of the aortic arch.

At birth the lungs become functional with the first breath taken: the foramen ovale therefore closes and the ductus arteriosus shrivels and becomes impervious. The site of the foramen in the inter-atrial septum is marked by a depression (fossa ovalis) and the former arterial duct remains as a ligament (ligamentum arteriosum).

During foetal life the lungs receive the blood necessary for their growth as organs from special arteries (bronchial arteries) from the aorta, and these vessels continue, after birth, to nourish with pure blood the actual lung tissue.

The enormous dimensions attained by the aorta are conveyed by the transverse section of this vessel from a Finner Whale, *Balaenoptera physalus* (fig. 25), but even in the biggest whales the aorta, like the heart, is not of excessive proportions in relation to the size of the animal.

Tyson (1680) was the first to describe the retia mirabilia of the Cetacea. Cole (1944) quotes Tyson's remarks: "There is scarce any Animal in which the Veines and Arteries are more curiously branched or more numerous than in this . . . they form a curious Net work, and afforded a very pleasant sight." These vascular networks are by no means exclusive to cetaceans; they are found also among the mammalia generally in such widely divergent groups as the sea-cows, the seals, the sloths, the armadillos, the anteaters and some of the rodents. It is only by virtue of their extreme profusion and development in the Cetacea that they are therein remarkable. Walmsley (1938) after discussing the peculiarities of the cetacean vascular system, including the retia mirabilia, sums up by saying that "they are not provisions for a possible shortage of oxygen, for a shortage does not occur, but . . . they are adaptations to the difference of pressure" to which the cetacean body is inevitably submitted. Earlier, Brazier Howell (1930) said much the same thing, though in less definite terms: "It seems that very little can yet

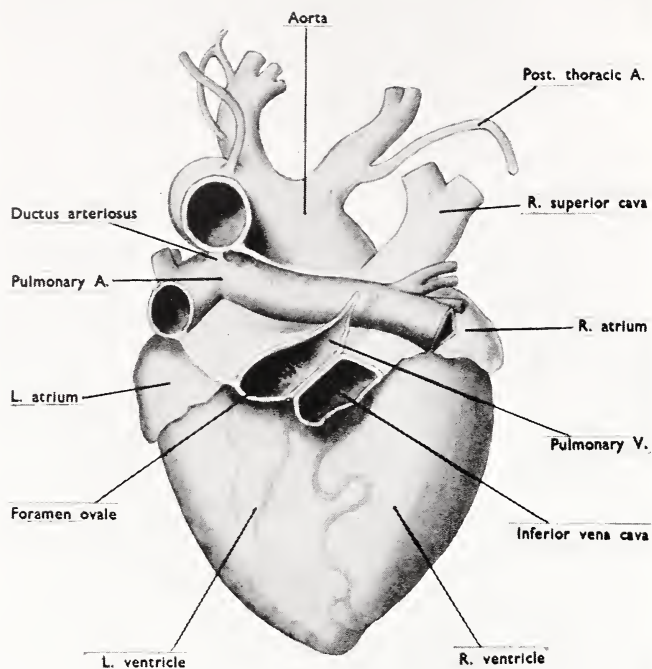


FIG. 23. Heart of a White-beaked Dolphin, *Lagenorhynchus albirostris*, seen from behind.

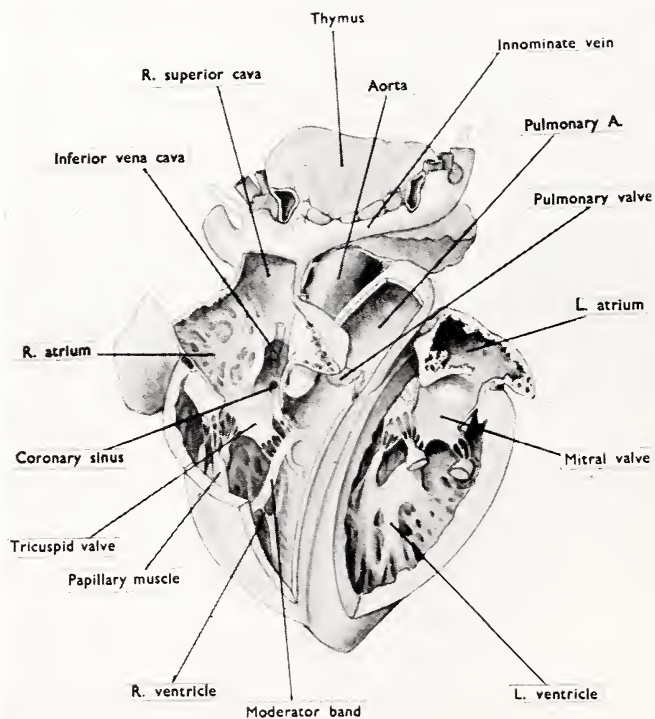


FIG. 24. Dissection of the heart of a Dolphin, *Stenella euphrosyne*.

be said except that possibly a diffuse type of retia might largely overcome any interruption of the blood flow that muscular or other pressure is capable of producing.”

On the assumption that during diving the muscles of whales like those of seals work in an approximately anaerobic state due to lack of circulation, Scholander (1940) adopts the working hypothesis of his collaborator Erikson that the retia might represent arterio-venous connections allowing the blood to be shunted past the muscles. This, it is remarked, would account for the observed absence of a diving brachycardia in the Cetacea.

Figure 26 shows the posterior wall of the chest (thorax) of a Common Porpoise. The lining (pleural membrane) has been removed from the right side to expose the underlying networks of small blood vessels (thoracic retia mirabilia) which, besides occupying much space between the heads of the ribs, extend into the spinal canal and connect the arteries of the chest wall with those supplying the brain. Figure 27 shows in diagrammatic form the relation of the arteries supplying the body wall to their associated retia mirabilia: the main trunks of these arteries pass through the network to supply the muscles and tissues of the chest wall but in their course give off (particularly the posterior thoracic artery) a number of minute branches which by subdivision form the meshes of the adjacent retial networks.

The plexiform rete mirabile from the thoracic blood system of a Finner Whale, *Balaenoptera physalus*, is shown in figure 28. The whole system is invested in a mass of fatty tissue.

The blood supply to the brain of a Common Dolphin, *Delphinus delphis*, is displayed in a dissection of both the dorsal and ventral aspects of the fore-part of the body (figs. 29 and 30). The dorsal view shows two large spinal meningeal arteries lying within the spinal canal, the bony arches roofing which have been cut away to expose the vessels. These arteries, which supply the brain with blood, have no direct connection with the heart or with the main systemic arteries but arise from the meshes of the thoracic and spinal retia mirabilia derived from the body-wall arteries. They pass into the cranial cavity at its posterior end providing blood to the cerebral arteries and to the ophthalmic retia mirabilia. Still another rete mirabile, the cervical rete, should be noted in the neighbourhood of the neck vertebrae.



FIG. 25. Transverse section of the aorta of a Finner Whale, *Balaenoptera physalus*. Diameter $5\frac{1}{2}$ inches.

The ventral aspect of the dissection shows the main blood vessels of the neck and chest. The heart has been removed, exposing to view the aorta which, from its origin at the heart, arches first dorsally and then tailwards. Parts of the further course of this main artery are to be seen in the dissection illustrated in figures 26 and 27. Two great vessels, the innominate arteries, have their origin from the aortic arch. (They cannot be seen in the dissection (fig. 30) but are displayed in the exhibit of the undissected heart (fig. 23), in which, it should be remembered, the arrangement of vessels is the reverse of that in figure 30 as the heart is viewed from behind, not from in front). The right innominate artery gives off near its origin a branch, the right posterior thoracic artery (see fig. 27), and a little further on it divides into the right subclavian and the right common carotid arteries. At the subclavian-carotid junction the transverse cervical artery arises. The subclavian artery, in passing ventral to the innominate vein, gives off the internal mammary artery. The subclavian artery is the root artery of the forelimb, to which it is principally distributed. The internal mammary artery passes tailwards deep to the ribs and outside the pericardium to supply the chest wall. The right common carotid artery divides immediately into external and internal carotids. In the dissection exhibited the external carotid artery has been cut short to expose the course of the internal carotid, which degenerates after birth since its original office of carrying blood from the heart direct to the brain is then usurped by the spinal meningeal arteries described above.

The arrangements of the corresponding vessels of the left side differ somewhat from those of the right. The disposition of the subclavian and the internal mammary arteries is similar, but the left posterior thoracic artery, instead of springing from the innominate artery, arises directly from the aorta. (In the dissection exhibited (fig. 30) a window has been cut in the bend of the aorta to show the exit therefrom of the posterior thoracic artery.) The left transverse cervical artery arises from the external carotid artery at some distance anterior to the division of the innominate into subclavian and common carotid arteries. A portion of the further course of the external carotid artery can be seen in the dissection shown in figure 40, likewise its division into internal maxillary and lingual arteries, to the face and tongue respectively.

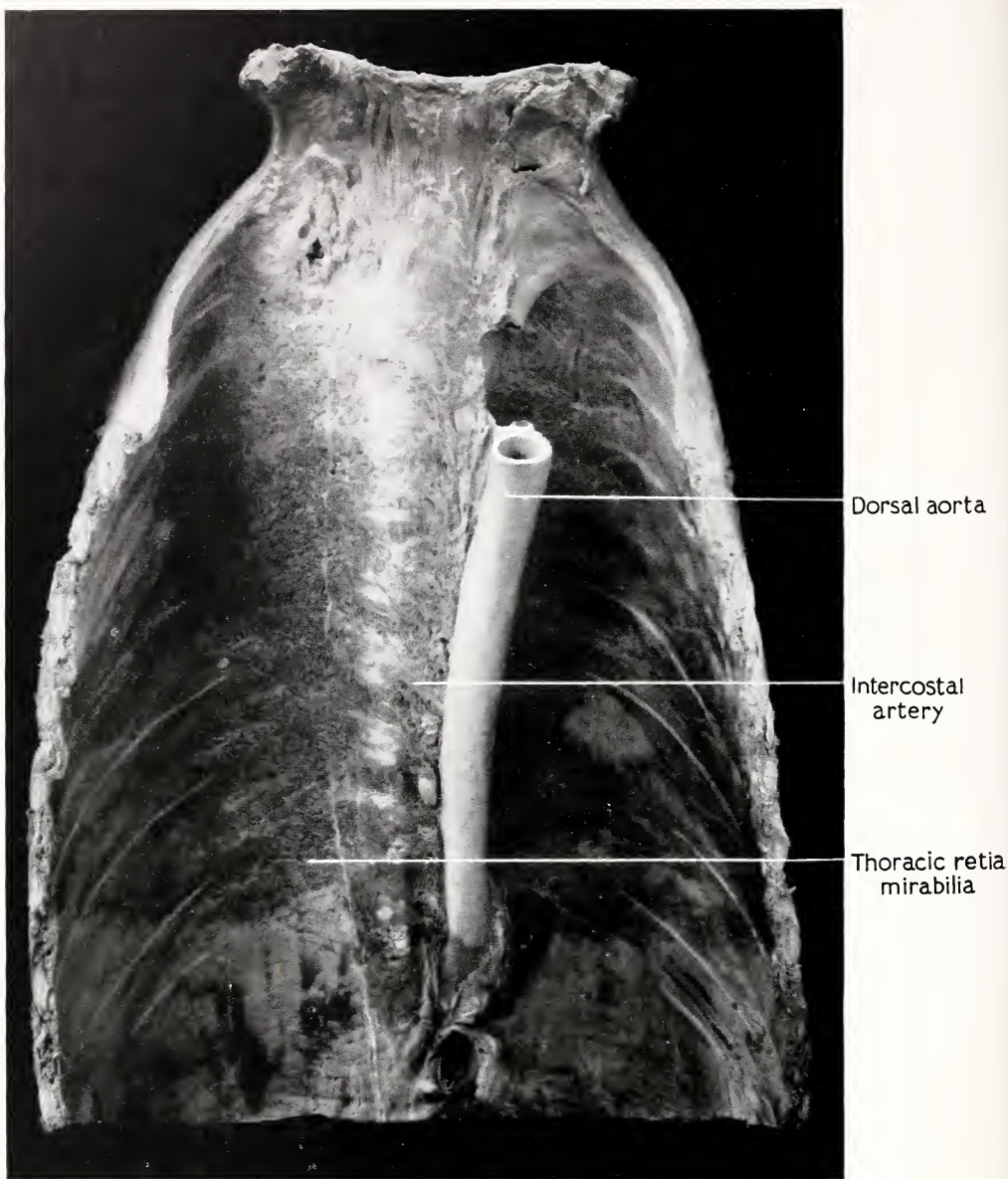


FIG. 26. Posterior wall of the chest of a Common Porpoise, *Phocaena phocaena*, showing, by the removal of its lining (pleural membrane), the position and extent of certain massive networks of small blood vessels (thoracic retia mirabilia) that extend into the spinal canal and connect the arteries of the chest wall with those that supply the brain.

The systemic veins are but partially displayed in the dissections exhibited, but attention may be drawn to certain of them. The dissection shown in figure 30 exposes the large innominate veins lying between the thyroid and thymus glands in close proximity to the aortic arch and to the innominate arteries. The left innominate vein is several times longer than the right (see also fig. 24) and each is formed by the union of veins carrying blood from the head, forelimbs and fore-part of the body, namely, the internal jugular, subclavian and posterior thoracic veins respectively. A portion of the last of these is shown in figure 27. The two innominate veins unite to form the superior caval vein which opens into the right atrium of the heart.

EXCRETORY SYSTEM

In the Cetacea the kidneys are of large size and are distinguished from those of most mammals by their extreme degree of lobulation. Each renal mass is in fact composed of a multitude of smaller kidneys (renules) bound together by a fibrous investment. Matthews (1950) has recently summarized the information about the number of renules composing the kidney in various kinds of Cetaceans; he finds that this number ranges from some 300 in a small dolphin, *Stenella frontalis*, to about 3,000 in a Blue Whale, *Balaenoptera musculus*.

Figure 31 shows part of the kidney of a Sperm Whale, *Physeter catodon*, dissected to expose the renules. One of these has been cut in half to show that it is a complete unipyramidal kidney with central medulla, peripheral cortex and medullary papilla traversed by a major duct opening into a ureteric calyx. Each renule has its own blood vessels, being supplied by the ramifying branches of the renal artery and drained by the superficial venous plexus and interlobular veins which unite to form the renal vein. Multiple collecting tubules from the renules convey the urine into the numerous branching calyces into which the anterior end of the ureter is divided.

The relation of the urinary system to the neighbouring organs is shown in the dissection of a Common Dolphin, *Delphinus delphis*, represented by figure 32. The peritoneum has been removed from the right kidney and from the pair of suprarenal (adrenal) bodies lying anterior to the kidneys.

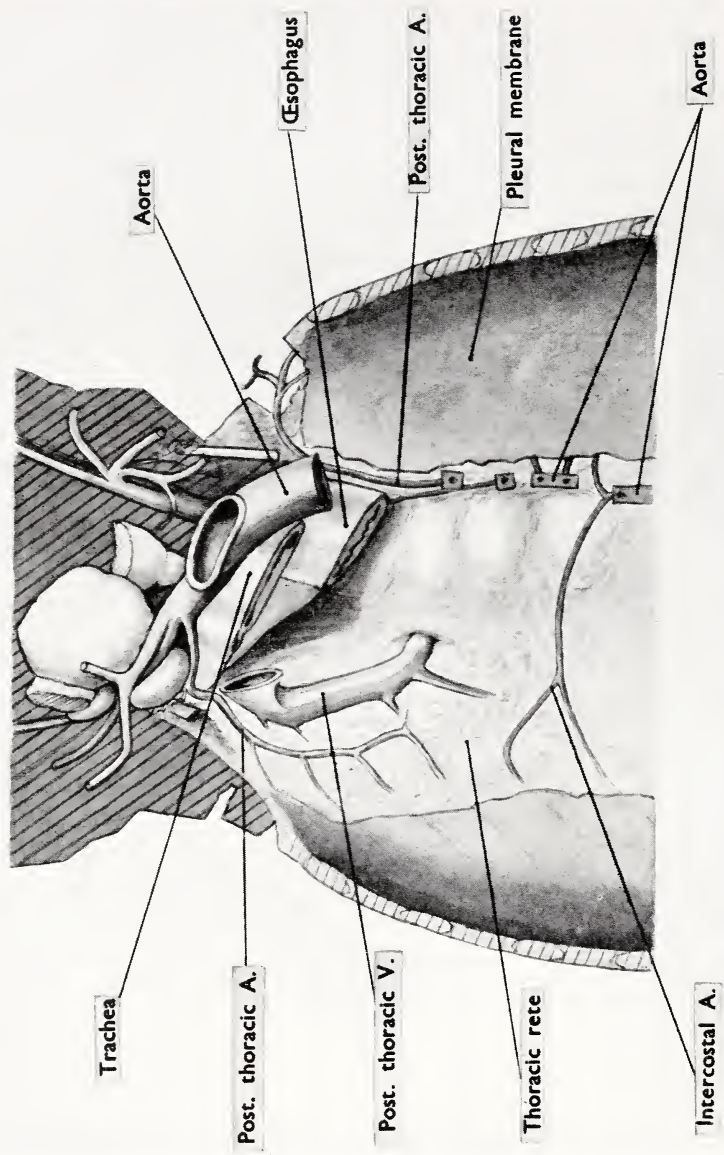


FIG. 27. Throat and posterior wall of the chest of a Common Porpoise, *Phocaena phocaena*, showing the relation of the arteries that supply the body wall (posterior thoracic and intercostal arteries) to the network of small blood vessels (retia mirabilia) associated with them.

The renal artery from the aorta and the renal vein to the inferior vena cava are situated near the anterior end of the kidney, while the ureter emerges near its posterior end. In this respect the cetacean kidney differs from that of most other mammals in which ureter, renal artery and renal vein all connect with the organ at the same region (the hilum) near its middle. The urine from the kidneys is carried to the bladder by a pair of muscular tubes (ureters), of which the right is exposed in the dissection. Each ureter passes into the bladder at a point about one-third of the way down that viscus from its anterior end. In its contracted state the bladder is fusiform in shape: it communicates with the exterior by a perineal urinary channel, the urethra.

REPRODUCTIVE SYSTEM

The reproductive system in the female cetacean is represented by two dissections shown in figures 32 and 33. In the first of these the ventral aspect of the reproductive organs of the Common Dolphin, *Delphinus delphis*, is shown, and in the other a partly dorsal, partly lateral, view of the corresponding region in a specimen of *Stenella euprosyne*. The female reproductive organs are situated, tailwards of the kidneys, at the hinder end of the abdominal cavity, in close proximity ventrally to the urinary bladder, and dorsally to the rectum. A median groove on the exterior ventral surface of the body towards the tail contains anteriorly the clitoris, immediately behind this the urethral opening, next the genital aperture (vulva) and lastly, at its hinder end, the anal aperture (anus or vent) of the alimentary canal. The vestigial pelvis in this vicinity should be noted. From the vulva a thick-walled tubular passage extends inwards and headwards dorsal to the bladder: this is the vagina whose cavity at its forward end becomes continuous with that of the unpaired hinder portion of the womb or uterus. The body of the uterus soon divides into two horns, to constitute the uterus bicornis of all Cetacea and of many other mammals. These uterine horns arch laterally and become continuous with the convoluted and much more slender fallopian tubes (oviducts), each of which at the end distant from the uterus opens out into a very wide fallopian funnel. The ovaries in the immature dissected specimens are smooth, bean-like bodies attached to the anterior free end of the broad ligament and each is partially



FIG. 28. Part of the thoracic blood system of a Fin Whale, *Balaenoptera physalus* with a portion of the surrounding tissue removed to show the convoluted nature of the vessels.

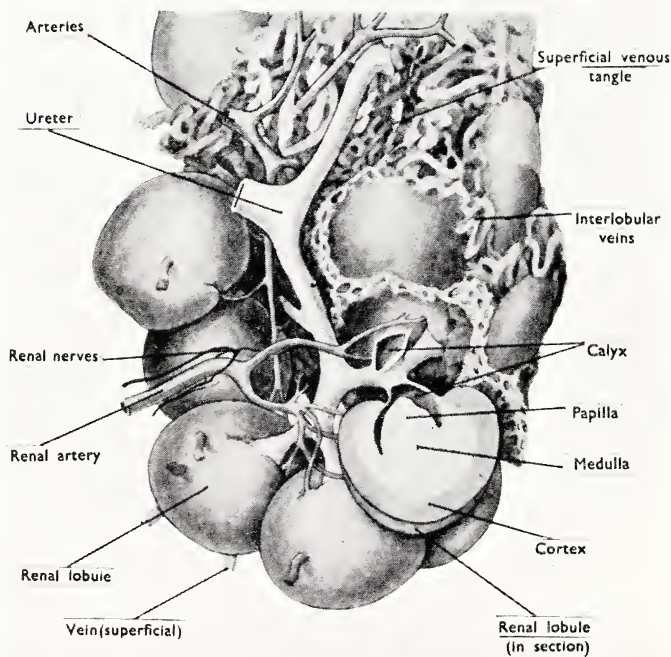


FIG. 31. Part of the kidney of a Sperm Whale, *Physeter catodon*.

covered by a sac-like development of the fallopian funnel, the bursa ovarii. The broad ligament is a prolongation of the peritoneum from the margin of the uterus to the side wall of the abdominal cavity. The round ligament is a narrow, flat, fibrous band lying in the broad ligament and extending posteriorly from the uterus near its junction with the fallopian tube to the abdominal body-wall.

The male reproductive system is not included in the exhibits as a separate dissection, but portions of it are exposed in the Common Porpoise represented by figure 2. Two features characteristic of all male cetaceans are demonstrated: the permanently intra-abdominal position of the testes and the retractile intromittent organ (penis) withdrawn into a pouch within the general contour of the body.

MAMMARY GLANDS

The mammary glands in female cetaceans are not detectable superficially save by their opening to the exterior. Each of the two nipples is situated in a cleft lying to one side of the genito-anal recess. A dissection of the mammary cleft of an adult Blue Whale, *Balaenoptera musculus*, is shown in figure 34. Although the nipple is withdrawn some distance within the general contour of the body (which may be assumed to be its usual position) it is believed that during suckling it is capable of protrusion so that it may be gripped by the mouth of the feeding calf. The two mammary glands extend forwards from the nipples, their long axes slightly divergent from the middle line of the body. In shape each is, in ventral view, an elongated oval though tapering more at its anterior than at its posterior end. The gland is of much greater width than thickness so that in side view its outline is rather spindle-shaped. The interior of the gland is similar in structure to that of other mammals, but it is provided with numerous large channels (galactophorous sinuses) for the milk secreted by the glandular tissue (parenchyma). The sinuses communicate with a spacious reservoir, the lacteal duct, in which the milk collects.

The gland lies between the muscles of the skin and those of the body and it is probable that the milk in the lacteal duct is forced through the nipple by the contraction of the surrounding muscles. Indeed, some such

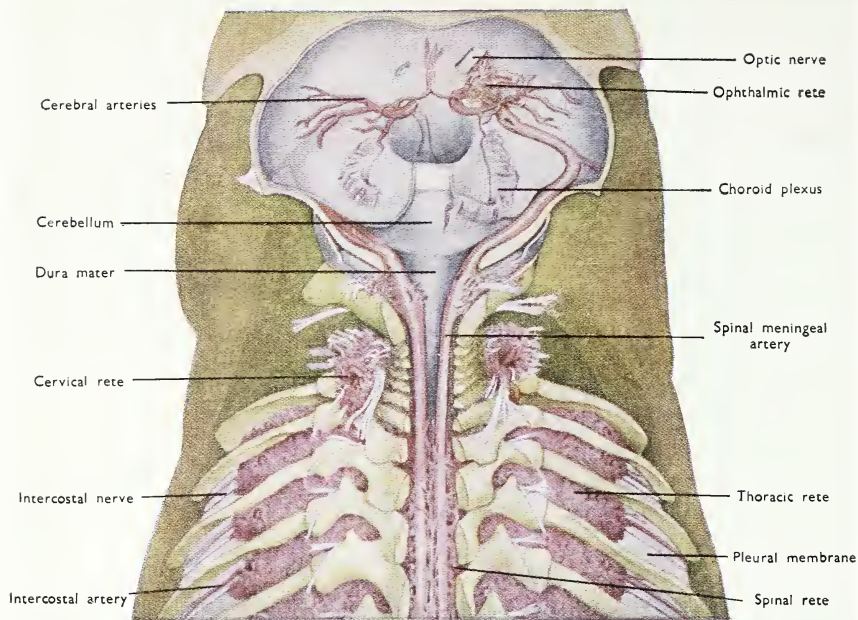


FIG. 29. Dissection of the back of a Common Dolphin, *Delphinus delphis*, to expose two large arteries in the spinal canal that enter the cavity of the skull and supply the brain with blood.

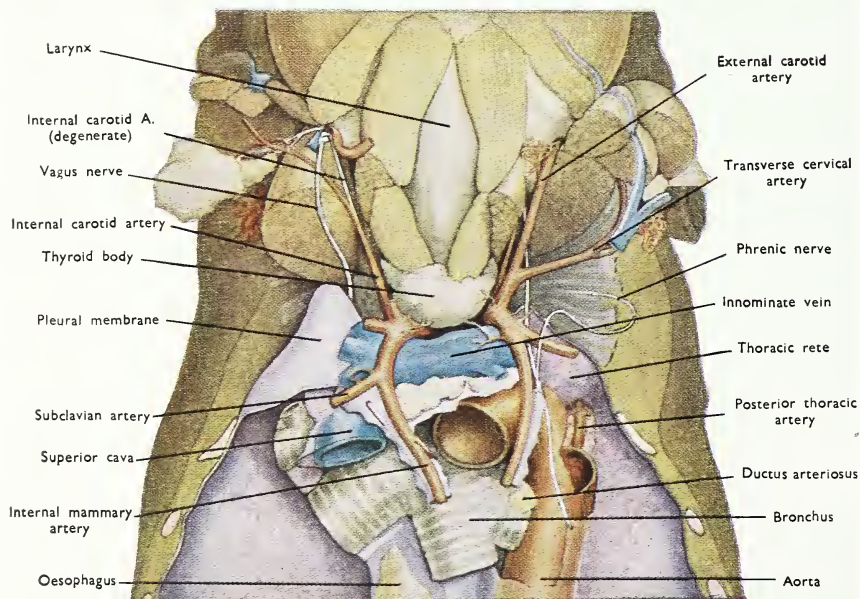


FIG. 30. Dissection of the lower surface of a Common Dolphin, *Delphinus delphis*, to expose the chief blood vessels in the neck and chest.

provision would seem to be essential, considering the conditions under which the parent whale is obliged to suckle its young.

It was mentioned earlier that the tongue of the adult Rorqual is degenerate, but this is by no means the condition in the suckling Rorqual calf. For in the calf it is provided with a strong, broad, muscular ridge along each side of its upper surface, with an intervening, gutter-like depression which widens out in front into a basin-like hollow behind the tongue tip. Moreover the calf palate, between the two "sides" of baleen, is not pronouncedly keeled as it is in the adult. It is believed that, when feeding, the suckling calf presses the tongue ridges to the palate, thus forming a tubular cavity which, when the calf applies its mouth to its dam's nipple, provides a passageway to the gullet for the milk and simultaneously prevents water from being swallowed.

NERVOUS SYSTEM

The brain is enclosed in, and protected by, the cranial portion of the skull (labelled "Skull" in figure 2). In the dissection represented by figure 1, the left half of the cranium has been removed, revealing the brain as closely packed within the cavity it occupies. At the hinder end of the brain-case is a large aperture (foramen magnum) through which the beginning of the spinal cord passes from the brain-stem into the neural canal. This canal is formed dorsally by a succession of bony arches (united by ligaments) springing from the bodies of the vertebrae, ventrally by the upper surfaces of the vertebrae themselves and their annectant intervertebral discs.

In the dissection shown in figure 36, the dorsal aspect of the brain is exposed by removal of the bones forming the top of the brain-case. The brain and commencement of the spinal cord are shown resting within their outer membrane (dura mater) on the floor of the skull and the anterior part of the backbone. The inner brain membranes (pia-arachnoid) are retained on the left side but have been removed on the right.

The brain conforms in general structure to the common mammalian pattern, but it is remarkable for its globular shape, for the complex convolution of its hemispheres and for the large size of the cerebellum, the region specially concerned with the regulation of automatic body movements.

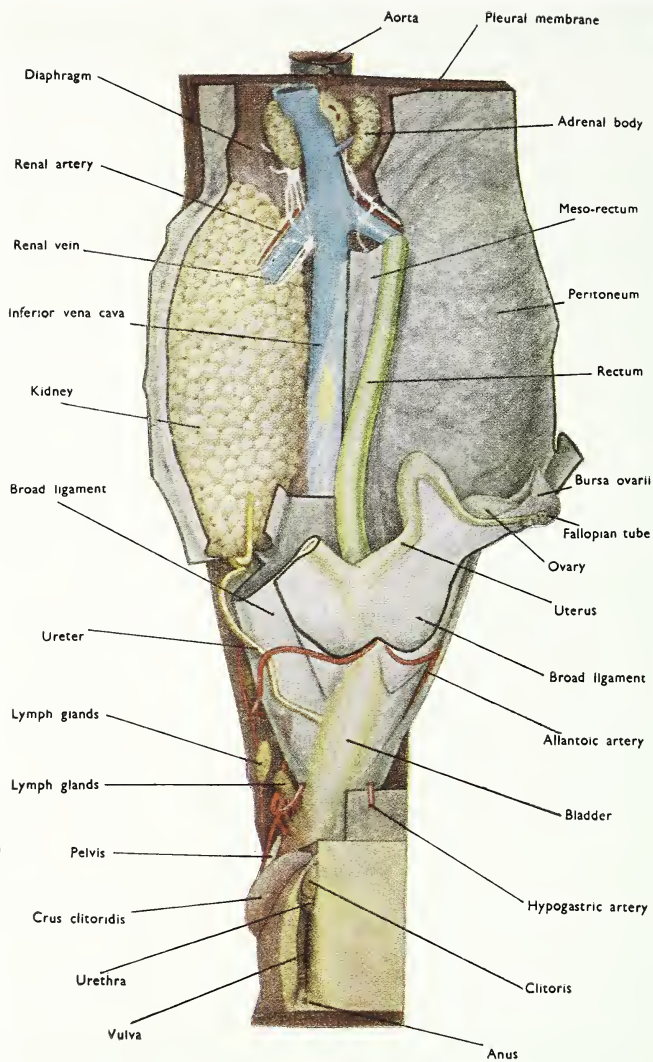


FIG. 32. Urinogenital system of a Common Dolphin, *Delphinus delphis*, to show the large size of the kidneys and their relationship to neighbouring organs,

The dissection of the brain of a Common Porpoise as seen from below (fig. 37) shows it resting within the skull-cap and outer brain membrane (dura mater); on the right side the innermost membrane (pia mater) has been left *in situ* and the ophthalmic rete surrounding the nerves to the eye is also displayed.

Three main parts of the brain are distinguishable in the dissection, viz., the cerebrum and cerebellum already mentioned, and the medulla oblongata. This last is that portion of the brain-stem lying below the cerebellum, and extending from the site of origin of the sixth pair of cranial nerves backwards to the foramen magnum. In front of the medulla oblongata and continuous with it is the pons Varolii: medulla and pons constitute the hind-brain (myelencephalon).

The cleft dividing the cerebral hemispheres from one another is the longitudinal fissure, and the conspicuous groove dividing each hemisphere into a front and a back portion is the Sylvian fissure.

The compression of the cetacean brain from front to back and the great enlargement of the cerebellum have resulted in the latter's coming into close approximation with the cerebral hemispheres, so that in the figure of the dissection the crura cerebri of the mid-brain (mesencephalon) are not visible. These are two large bundles of nerve fibres which, issuing from the front margin of the pons Varolii, diverge and pass one into each half of the cerebrum (fore-brain, prosencephalon). In the dissection itself the pons is more obvious than would appear from figure 37. It is a convex area of the hind-brain situated behind the pituitary gland and is of about the same breadth as that body. Its hinder limit is determinable by the origin of the sixth cranial nerves which emerge from the brain-stem at the junction of pons and medulla. The constituent fibres of the pons connect the two halves of the cerebellum and relay to the cerebellum nerve impulses coming down from higher centres in the mid-brain and fore-brain.

The organs of smell are completely absent in members of the dolphin family and with their disappearance has gone also the first (olfactory) pair of cranial nerves. Thus the optic nerves are the foremost pair seen in the dissection of the ventral surface of the brain. The course of these nerves is somewhat obscured by the pituitary body but, as in other mammals, there is

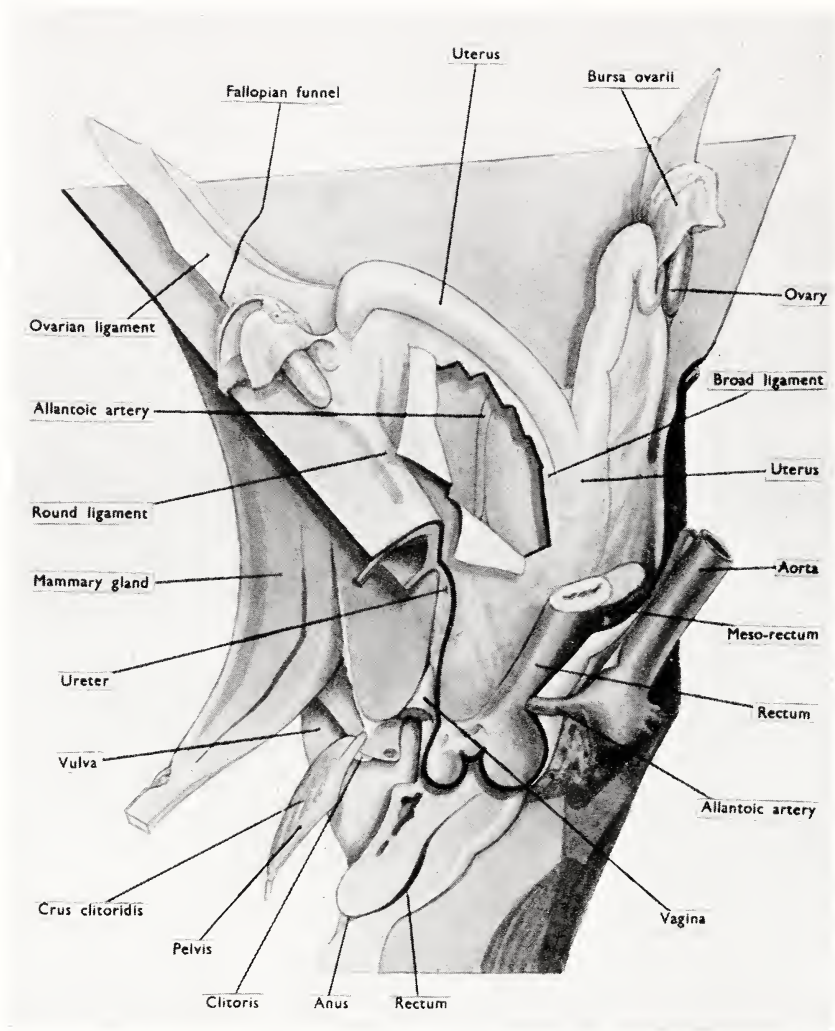


FIG. 33. Female genitalia of a Dolphin, *Stenella euphrosyne*.

within them a partial crossing over of retinal nerve-fibres from their origin in one eye to visual centres situated in the opposite half of the brain. In the figure the structure on the left side labelled "optic tract" is composed principally, but not entirely, of retinal nerve-fibres from the right eye: some nerve-fibres from the left eye are also incorporated in the left optic tract, and so similarly on the right side. The two optic nerves effect this interchange of contained fibres at the optic chiasma, whence the rearranged visual fibres proceed backwards to the brain as a stout bundle on each side, known as the optic tract. The third (oculomotor), fourth (pathetic), and sixth (abducent) nerves supply the muscles of the eyeball and are all comparatively slender. The third nerve leaves the mid-brain just in front of the pons Varolii on the inner side of the crus cerebri. The fourth nerve takes origin from the roof of the mid-brain and so is not visible in the dissection. The sixth nerve arises near the front end of the medulla, on the ventral surface of the hind-brain.

The fifth pair of cranial nerves (trigeminal) have their origin from the side of the pons Varolii near its anterior end. As the name implies the nerve has three branches, (1) ophthalmic, which is purely sensory, to the orbital and part of the nasal region, (2) the maxillary, which is sensory, to the upper jaw, and (3) mandibular, both sensory and motor, supplying the muscles, skin and teeth of the lower jaw.

The seventh (facial) nerve arises from the medulla and supplies the muscles of the facial region. A portion of the onward course of the nerve on the left side can be seen in figure 41 as it passes external to the tympanic bulla and forwards underneath the orbit.

The eighth (auditory) nerve arises in close proximity to the seventh, i.e., immediately behind it on the side of the medulla. It is a nerve of special sense, its fibres conveying impressions of hearing from the internal ear to the brain. In correlation with the importance of the sense of hearing to cetaceans, these nerves are of robust size and Kellogg (1938) has remarked that in the dissected brain of a Bottlenosed Dolphin, *Tursiops truncatus*, the central nervous mechanism for the reception and disposal of cochlear (auditory) stimuli was also highly developed, in contrast to the less well developed optic mechanism.



FIG. 34. Longitudinal section through the mammary cleft of an adult female Blue Whale, *Balaenoptera musculus*, showing the nipple of the mammary gland lying entracted within it.
A rod is passed through the milk duct which traverses the nipple.

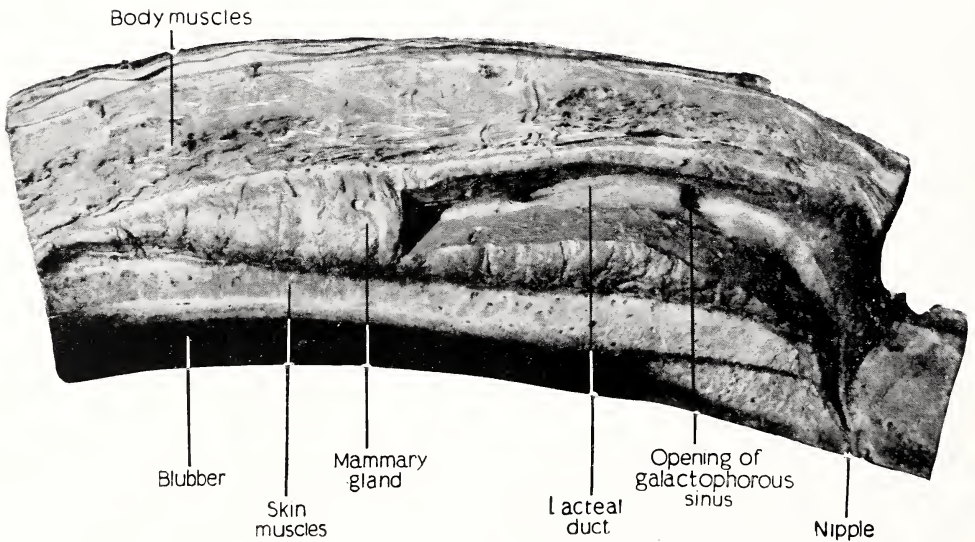


FIG. 35. Left mammary gland of a female Common Dolphin *Delphinus delphis*, exposed by the removal of skin and muscles.

The ninth (glossopharyngeal) nerve (having its origin on the side of the medulla between the eighth (auditory) and the tenth (vagus) nerves) supplies the pharynx and sends a branch to the hinder part of the tongue. The tenth (vagus or pneumogastric) nerve arises from the brain by several rootlets, which unite to form a single trunk, which, with its numerous visceral branches, has an extensive distribution, supplying the gullet, stomach, larynx, bronchi and lungs. A part of its course is shown in figure 30 and also, unlabelled, in figure 1.

The eleventh (spinal accessory) nerve is partly associated with the vagus and partly with the spinal cord: it is thus both cerebral and spinal in origin. Its cerebral portion passes into the vagus nerve for distribution therewith and its spinal fibres are distributed to certain muscles of the shoulder.

The twelfth (hypoglossal) nerve arises from the ventral side of the medulla by several rootlets, which join to form a single trunk: this passes forward (see fig. 41) to supply the muscles of the tongue, and, indirectly, certain muscles in the neck.

Finally, the dissection shows two pairs of the spinal nerves attached to the sides of the spinal cord, the first of the succession of nerves which continues along its length, as shown in figure 1. This dissection shows also the brachial plexus, that group of closely associated cervical spinal nerves, the roots of which, originating separately, merge to form a series of connections of irregular size before their final distribution to the forelimb. The phrenic nerve is exposed in the same dissection to show its course to the diaphragm, which it supplies as a motor nerve.

SPECIAL SENSE ORGANS

In the Cetacea the sense organs have undergone very considerable modification from the orthodox pattern found in terrestrial mammals. The olfactory sense is almost or entirely absent. The Whalebone Whales have a few perforations of the mesethmoid bone corresponding to the cribriform plate of unspecialized mammals, but the olfactory nerves are simple and after passing through these perforations are distributed to the membranes of

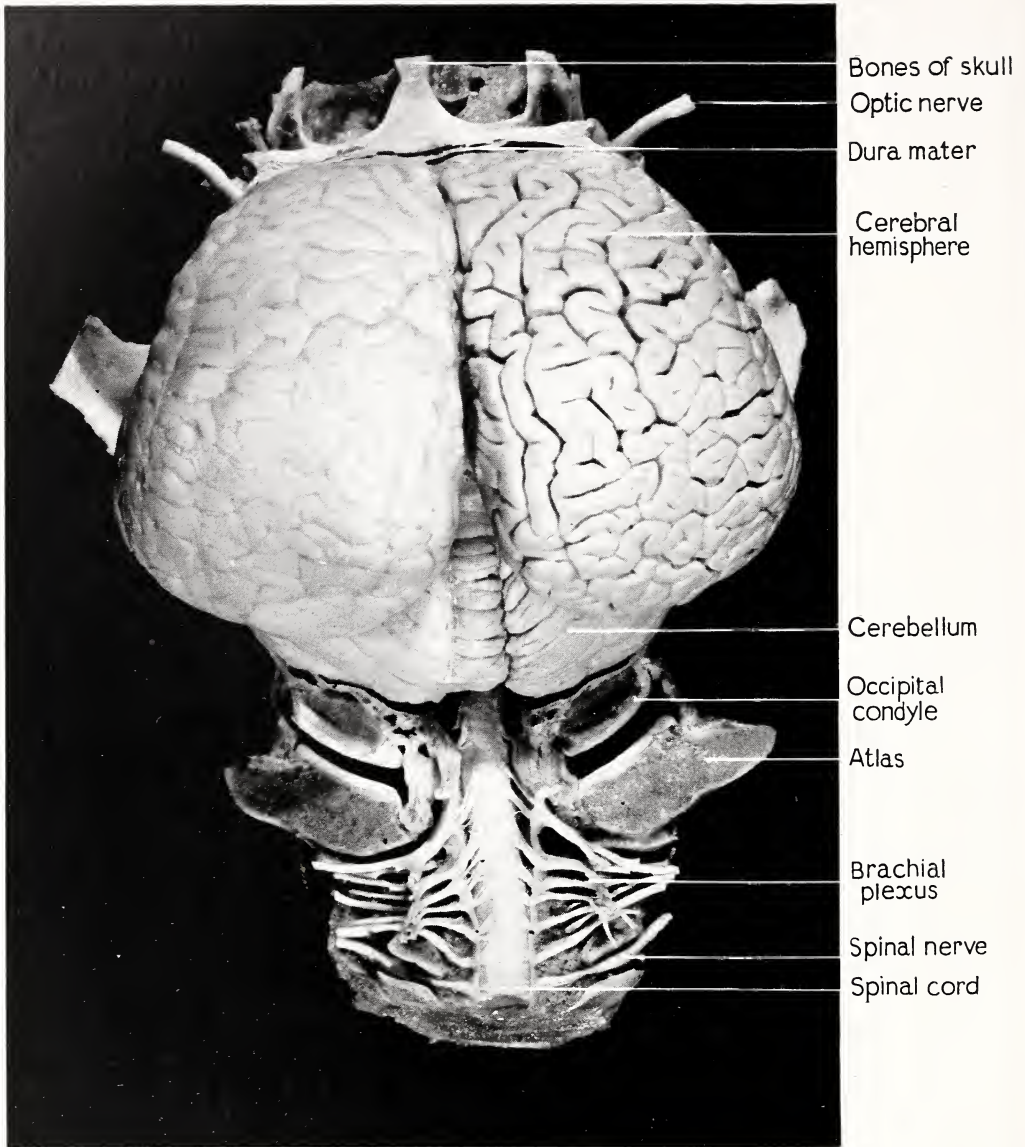


FIG. 36. Brain and commencement of the spinal cord of a Common Porpoise, *Phocaena phocaena*, seen from above, resting within their outer membrane (dura mater) (cut short) and the floor of the skull and back bone. The inner brain membranes (arachnoid and pia mater) are retained on the left side, but removed from the right.

the nose passage. In the Bottlenosed Whales a single pair of holes is all that remains of the foramina of the cribriform plate, while in the dolphins there are no perforations and the olfactory nerves have completely atrophied (see fig. 37).

A section through the eye of a Blue Whale, *Balaenoptera musculus*, is shown in the dissection represented by figure 38. In comparison with the eyes of terrestrial mammals, the cetacean eye manifests various adaptations to submarine life. These include the strong convexity of the lens and the shallowness of the posterior segment of the globe as modifications to meet aquatic optical conditions. Provisions against the high pressures of deep water are represented by the thickened margins of the cornea, the enormous increase in thickness and density of the sclerotic capsule ⁽¹⁾ and the encasement of the optic nerve in a massive sheath of connective tissue and blood vessels (ophthalmic rete). Kellogg (1938) draws attention to other adaptations, which, although not obvious in the dissection, merit mention. The cetacean tear (lachrymal) gland exudes a greasy instead of a watery substance to protect that portion of the eye exposed to sea-water. The exterior mucous coating of the eye (conjunctiva) is replaced in a number of different kinds of whales by a horny epithelium. Finally to protect the eye against continuous cooling at temperatures below the normal body temperature, the liquid refractive media within the eyeball are so constituted as to have a lower freezing point and there is also provision for an accelerated inflow and outflow of the liquid in the anterior ocular chamber.

In the absence of external ears (pinnae) the Cetacea demonstrate another modification correlated with the assumption of an aquatic mode of life. The aperture leading into the external auditory meatus is flush with the surface of the body. Vestiges of the auricular cartilage buried beneath the skin of some porpoises and of two external ear muscles in Whalebone Whales are all that remain in the way of evidence of the former existence of external ears.

⁽¹⁾ But G. L. Walls in "The Vertebrate Eye" (Michigan, 1942), puts forward quite the opposite view. He says, p. 416: "The mere fact that the whales' cornea is relatively thin—though completely exposed to water is itself enough to show that the thickness of the sclera can have no relation to pressure as such. But the differential pressure upon various areas of the cornea, due to wave action, to ordinary swimming movements, and the quick changes in speed and direction would deform so thin a cornea on so large an eyeball were that cornea not supported peripherally by an immensely stiffer structure—just as a plastic watch-glass is supported by its unyielding metal bezel."

"While a grape keeps its rotundity merely while lying on a table, it would flatten out and burst if it were magnified to the size of a house—unless that is, its skin were thickened *out of proportion*. The inordinately thick scleras of large whales and the biggest sharks are no thicker than need be. They are a logical result of making a soft tissue optical instrument almost too large for rigidity in the face of the buffetings of the severe aquatic environment. The great whales would still need their thick scleras, even if they never left the surface at all."

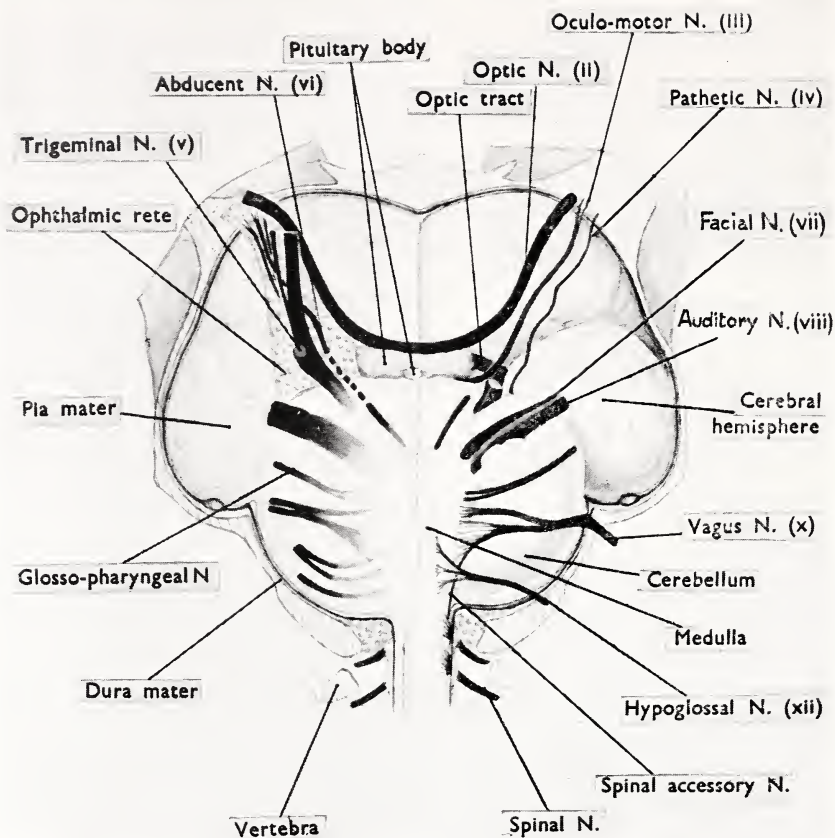


FIG. 37. Brain and commencement of the spinal cord of a Common Porpoise, *Phocaena phocaena*, seen from below, resting within the skull cap and outer brain membrane (dura mater).

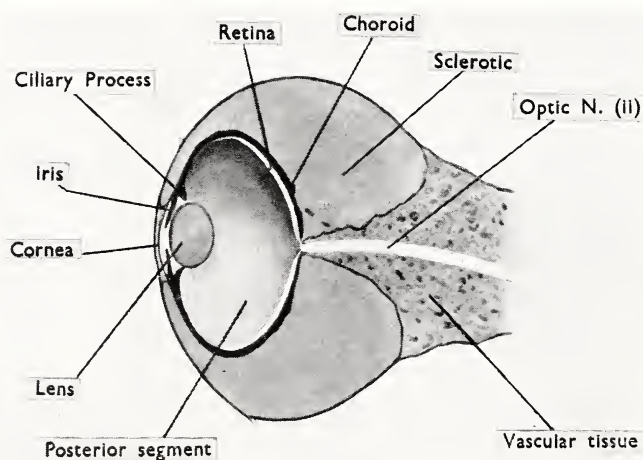


FIG. 38. Diagram of the eye of a Blue Whale, *Balaenoptera musculus*, in section.

Figures 39 and 41 show the external auditory meatus in Whalebone and in Toothed Whales. It will be noted that in the Finner Whale the earhole leads towards the eardrum (tympanic membrane) through a short funnel-shaped passage into a minute auditory tube which widens out again in the vicinity of the drum to accommodate that peculiar structure (fig. 40). Kellogg (1938) points out that the meatus in Whalebone Whales may be completely closed near its middle. In the Toothed Whales the meatus is most constricted at its external end, where it is of pin-hole size, and it gradually increases in diameter towards the tympanic membrane.

The shape and disposition of the tympanic membrane of the Whalebone Whales is quite unlike that of any other mammal. Unlike the more usual, fairly taut, more or less vertically disposed membrane, the drum projects along the external meatus as an elongated, hollow conical structure, in large whales some $2\frac{1}{2}$ –3 inches long. At its outer end it is capped by a still longer plug of wax. The tympanum of the Toothed Whales is more akin to that of the generality of mammals, being only very slightly convex outwards.

Interposed between the outer and inner ear is the middle ear (tympanic cavity) with its contained chain of auditory ossicles linking the one to the other. These ossicles are the hammer-bone (malleus), anvil-bone (incus) and stirrup-bone (stapes), articulating in that order from without inwards. The malleus is connected with the eardrum (in the Mysticeti by a ligament which extends along the length of the conical tympanum internally before terminating on the malleolar manubrium), and it is firmly fused by its processus longus to the lip of the tympanic bulla. The stapes is wedged in an oval window in the innermost wall of the middle ear (the fenestra ovalis) and all three ossicles combine to form a rigid, irregular column between tympanum and periotic.

The tympano-periotic bones are themselves noteworthy. They are composed of the densest bone to be found in the cetacean skeleton and so persist in fossil deposits when all other traces of the creatures to which they belonged have disappeared. The form of the tympanic bulla in Whalebone Whales can be seen in figure 40. It is attached to the periotic by two slender, flattened pillars of bone, while the periotic is firmly fixed amid the adjacent bones of the skull by tenon-like processes and is completely excluded

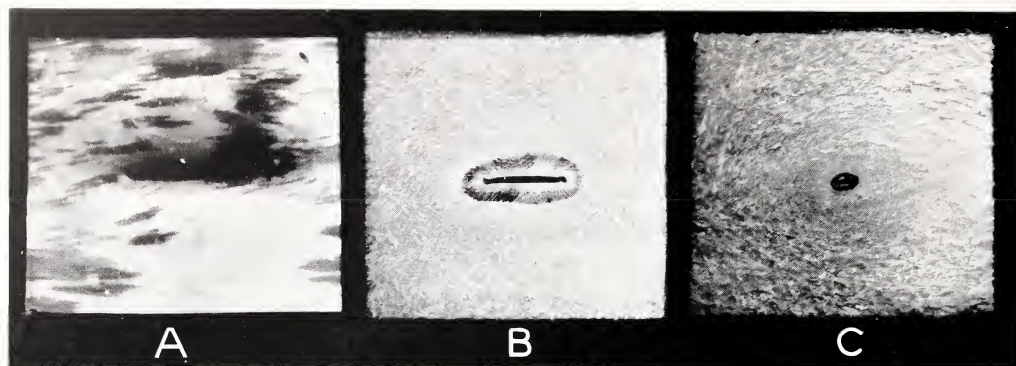


FIG. 39. Earhole and commencement of the auditory passage of a Finner Whale, *Balaenoptera physalus*. The earhole (A) is a small perforation situated behind the eye, leading through a short funnel-shaped depression (B) into a minute auditory passage (C).

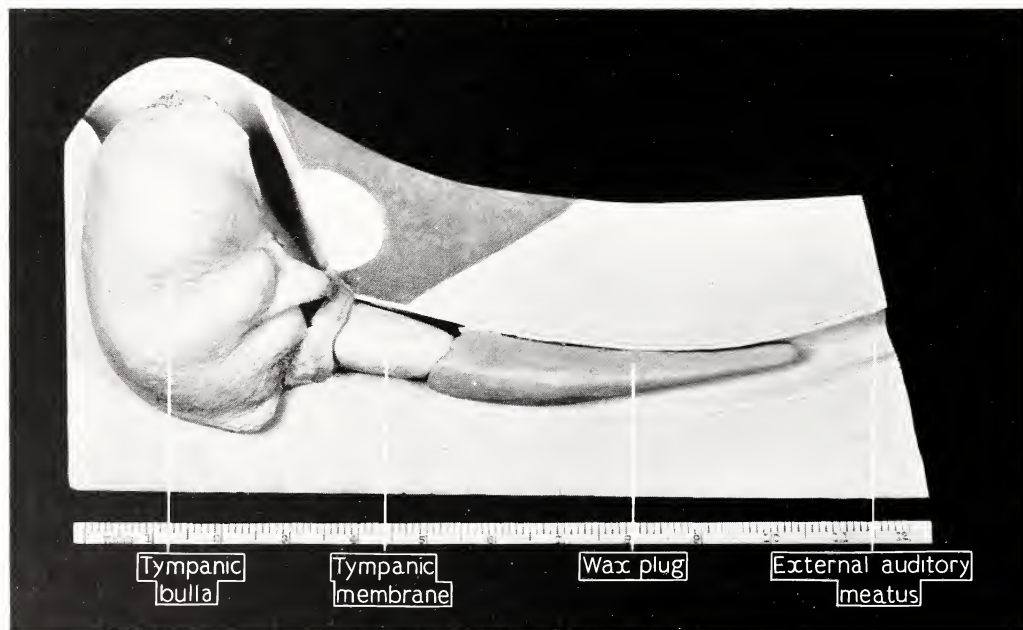


FIG. 40. External ear passage and tympanic bulla of a Finner Whale, *Balaenoptera physalus*, showing the tympanic membrane and the wax plug external to it.

from the cranial cavity by a considerable distance. This is in contrast to what is found in the dolphin family (Delphinidae). Therein the tympano-periotic has a ligamentous attachment only to the surrounding skull bones. In a groove between the squamosal and exoccipital, a tongue-shaped bony process unites the tympanic to the periotic bone. This process according to Flower (1885), "resembles in its relations the mastoid of ordinary mammals but in young Cetaceans it may be seen to be composed of two nearly equal parts, in close apposition with each other, the inferior being derived from the tympanic and the superior from the periotic, so that the latter alone can represent the 'pars mastoidea' of other mammals." The condition existing in the family of Toothed Whales known as the Bottlenosed or Beaked Whales (Ziphiidae) is intermediate between that of the Whalebone Whales and the Dolphins. In these animals whilst the general form of the tympano-periotic region is similar to that of the Toothed Whales generally, the tongue-shaped process is "greatly elongated and laminated, being composed of a large number of distinct thin plates, only held together by their common attachment to the tympanic. These fit into grooves between the squamosal and exoccipital, their extremities appearing on the outer surface of the skull, and they serve to attach the petro-tympanic more firmly to the cranium than is the case in the other Toothed Whales" (Flower, loc. cit.).

In referring to the olfactory sense a progressive deterioration of the olfactory system was noted from the Whalebone Whales through the Beaked Whales to the Dolphins. Similarly an increasing dissociation of the ear-bones from the adjacent bones of the skull is evident in these same cetacean families and in corresponding order. This again can be correlated with the specialization of the eustachian system. In most mammals the eustachian canal is a simple tubular structure, connecting the middle-ear cavity with the naso-pharynx. In the Whalebone Whales a large diverticulum or sac (pterygoid sinus) from the eustachian tube is found in the region of each pterygoid bone; in the Beaked Whales this sinus is, comparatively speaking, enormously enlarged, so that it completely occupies the lateral depression of the massive pterygoid bone. The Dolphins exhibit the extreme of specialization of the eustachian diverticula. Figure 41 shows the extension of the system which occupies the cavity of the pterygoid bone, but this

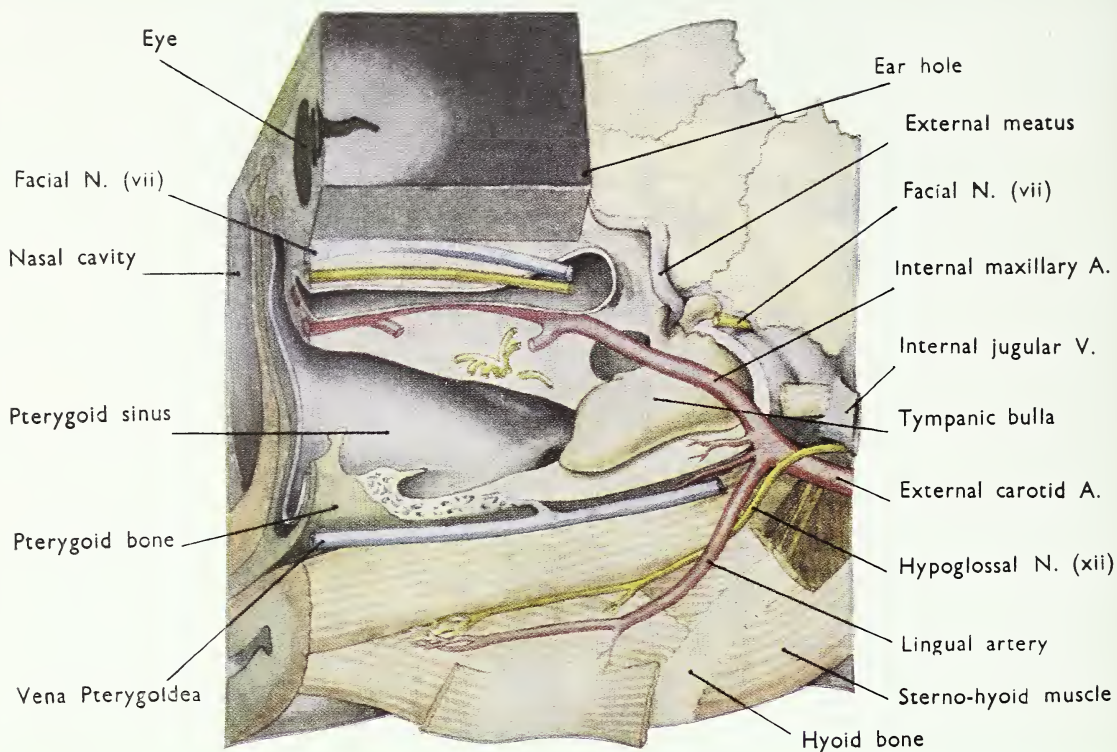


FIG. 41. Dissection of the auditory region of the head of a White-beaked Dolphin, *Lagenorhynchus albirostris*, showing the course of the passage (external meatus) that leads from the minute earhole to the ear bone (tympanic bulla) within which lies the chain of bones that connects the eardrum (tympanic membrane) with the actual organ of hearing (membranous labyrinth).

extension is only part of a highly complicated arrangement of sacs which occupies much of the palatal region. Two diverticula extend along the roof of the mouth, one on each side of the palate, reaching in the Common Dolphin to within an inch or so of the snout tip. This highly specialized eustachian arrangement in the Delphinidae, when correlated with the separation of the ear bones from bony contact with the adjacent cranial elements and with the complete atrophy of the olfactory sense, is suggestive of a dependence on the auditory sense as a means of maintaining contact with the external environment, to an extent not encountered in the rest of the Mammalia.

The inner ear is not demonstrated in the dissections shown, but it may be noted that the membranous labyrinth, while manifesting the different parts common to the Mammalia generally, has the cochlea (which contains the auditory end-organ) greatly enlarged relative to the semi-circular canals (which contain the end-organ of equilibrium). This arrangement may be still another indication of the important part hearing plays in the reception of external impressions in the Cetacea.

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